MOUNTAIN GORILLAS IN THE VIRUNGA VOLCANOES: ECOLOGY AND CARRYING CAPACITY

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To my many Rwandan friends and colleagues, those who have died, those who have fled and those who struggle on, that they should not be forgotten amidst all this talk of gorillas.

ABSTRACT

This study investigated the ecology of mountain gorillas (*Gorilla gorilla beringei*) across the Virunga volcanoes in central Africa. The main aim was to obtain an improved understanding of patterns of habitat availability, quality and utilisation by gorillas, in order to estimate the carrying capacity of the Virungas. Carrying capacity was defined as the number of gorillas which could be supported by the area, without significant degradation of the environment or loss of condition in the gorillas themselves.

The definitions and use of the term carrying capacity are reviewed in Chapter 1, along with the main approaches which have been taken to its measurement. The Virunga population and previous studies based at the Karisoke Research Centre are introduced. The conservation history of the population is described, and the need for a broader based study of gorilla ecology across the Virungas is highlighted. The approach taken to measuring carrying capacity in this study is explained.

In Chapter 2 a classification of habitat types within the Virungas is described, a habitat map is presented and the overall availability of these habitats is measured. The availability and distribution of gorilla foods within each habitat are investigated. It is shown that there is considerable variation between habitat types both in gorilla foods available and in the overall biomass, richness and diversity of foods.

Chapter 3 investigates the patterns of use of the available habitats by gorilla groups. Data are presented on the home ranges of six groups monitored by trackers and guides, and the relationships between group size, home range size and food density are investigated. The patterns of habitat selection within the home ranges of two groups are presented in more detail. Mountain gorillas were found to use a wider range of habitats than previously documented. Group size was found to be positively correlated with food density and home range size. The main study group used habitats selectively, in a way which could partly be related to habitat quality.

The diets of two groups occupying contrasting habitats are examined in Chapter 4. The responses of the two groups to different levels of food availability are compared, in terms of dietary diversity and selection. The accuracy of different methods of measuring dietary intake are compared. Both groups showed similar overall patterns of dietary selection. The group occupying habitats with a lower food availability showed a broader diet.

Chapter 5 investigates the effects of human disturbance on the gorilla population. Data on the distribution of gorilla groups and illegal use (poachers' snares) from the most recent census are presented, and the relationships between signs of illegal human use, snare density and signs of gorilla use, surveyed at a sample of sites across the Virungas, are investigated. A negative correlation was found between signs of gorilla use and signs of illegal human disturbance, indicating a negative impact of disturbance on the population.

Chapter 6 uses the information on the availability of habitats and their use by gorillas presented in previous chapters to make estimates of the number of gorillas that the area could support, using several different methods. It is shown that the Virungas could support a population of at least 600 individuals. The value and management implications of these estimates are discussed.

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DECLARATION

Tracker and guides monitoring the research and tourist groups on both the Rwandan and Zairean sides of the Virungas collected basic ranging data on these groups. Data from previous censuses was made available to me by C.R. Sholley and A.L. Vedder. I made use of regression equations relating plant height to leaf biomass provided by A.J. Plumptre. With these exceptions, I declare that all the data presented in this thesis was collected by myself, with the help of several Rwandan assistants. The analysis was undertaken in Bristol by myself, under the supervision of Professor S. Harris. No part of this work has been submitted for consideration for any other degree or award.

Alastair John McNeilage.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 CARRYING CAPACITY IN WILDLIFE MANAGEMENT

As more and more habitats around the world are lost through deforestation, desertification and conversion to agriculture, an ever increasing proportion of wildlife exists within the confines of protected areas, including national parks and other categories of reserve. While efforts can be made to allow humans and animals to coexist in areas inhabited by humans, this will not be possible for all species. The protection and management of wildlife within such protected areas is thus becoming more and more important. In considering the establishment of new protected areas and the management of existing ones, one of the most important issues for any endangered species is always whether the area can support a viable population, that is a population capable of long term persistence and evolutionary adaptation. This issue can be split into two questions, the first of which is how large does a population of that species need to be in order to be viable? This question has been a major focus in conservation biology in recent years (Soulé, 1987; Caughley, 1994), and various techniques have been proposed for establishing minimum viable population sizes. The second question is then how large an area is needed to support that number of individuals? This will, of course, depend on how many individuals a given area of the habitat concerned can support, that is on the carrying capacity of that habitat.

The concept of carrying capacity is important in wildlife management for several other reasons (Fowler & Smith, 1973; Bell, 1984; Caughley & Sinclair, 1994). Carrying capacity is widely used to evaluate and compare different areas as wildlife habitat (Hobbs & Swift, 1985). Where the goal of management is to preserve,

comparing the actual population size to the carrying capacity, that is the potential population size in that area, allows the success of conservation efforts to be assessed. Where the goal is to harvest animals, determination of the carrying capacity is an important aspect of determining the population size and cropping regime which will give the maximum possible sustainable yield (Caughley, 1976). Where a population in a confined area is growing or where loss of habitat has caused an existing population to be compressed into a small area, an estimate of how many individuals can be sustained by that area is vital to managers deciding, for example, if and when to cull.

The concept of carrying capacity has been the centre of considerable confusion in the ecological literature, and is notoriously difficult to estimate. A quote from Bell (1984) aptly describes the problem:

> *"The estimation of carrying capacity is the graveyard of ecological reputations. It is easy to be wrong; it is easy to be shown to be wrong; and being wrong can be expensive."*

However, given that carrying capacity is so central to wildlife management, it is important that the issue be addressed. This thesis investigates the ecology of mountain gorillas (*Gorilla gorilla beringei*) across the Virunga volcanoes, with the overall aim of estimating the carrying capacity of the area. This chapter will firstly review the definitions and uses of the term carrying capacity which have been put forward in the ecological literature, along with some of the approaches that have been taken to measure it. The Virunga gorilla population and the problems it faces will then be introduced, and the aims and structure of the thesis described.

1.1.1 Carrying capacity: definitions and uses of the term

Definitions and uses of the term carrying capacity have been reviewed by Bell (1984), Macnab (1985) and Dhondt (1988), and are summarised here. This discussion is primarily concerned with carrying capacity in the context of a plant-herbivore system. The term originates from the field of range management where it refers to the number of stock a range can support for a definite period of grazing without injury (Hadwen & Palmer, 1922; cited in Dhondt, 1988). It was first used in the ecological literature by Leopold (1933) and Errington (1934), with two different meanings. Leopold (1933) defined carrying capacity as the population density reached in a particular site where the population is limited by external factors. This he distinguished from the saturation point, which is the maximum density which can be reached by a species anywhere, under optimal conditions where the population is limited by intraspecific interactions. Errington (1934), however, defined carrying capacity as the "threshold of security" above which surplus animals are very vulnerable to predation.

From a theoretical point of view, carrying capacity has been defined as the equilibrium value of the logistic model of population growth, *K*. Odum (1953) was the first to use this definition and most ecological text books have followed this use. At a broad conceptual level, it is reasonable that the equilibrium value of the logistic, being the level at which the population would be expected to be regulated by whichever resources are limiting, should correspond to the maximum number of individuals that habitat could support in a sustainable way. However the logistic model assumes a closed, deterministic system, whereas most real populations are open and stochastic. Few wildlife populations have been shown to reach a constant equilibrium, most fluctuate within a varying range around a mean value (Caughley & Sinclair, 1994). This precise theoretical definition of carrying capacity is, therefore, of limited value to wildlife biologists. Although the logistic model can be useful, for example in predicting maximum sustainable yields (Clark, 1981), it does not take

account of intrinsic oscillations of populations, environmental fluctuations, emigration and immigration, and predation.

The most widely used definitions of the term used today are probably those of Caughley (1976, 1979). He argued that plants and herbivores form a system in which the rate of increase of plants is determined by the density of the animals eating them, and the rate of increase of the animals is determined by the density of the plants. An equilibrium is expected at which the rate of production of forage is equal to the rate at which it is consumed by the animals. The ecological carrying capacity is defined as the natural limit of a population set by resources in a particular environment, that is the equilibrium reached without external intervention. This can be thought of abstractly as equivalent to the K value of the logistic equation. The economic carrying capacity, on the other hand, is that population level that produces the maximum sustainable yield for cropping purposes and is thus a contrived equilibrium held in place by human intervention. It corresponds to the level at which the rate of population increase is highest and as such will be considerably lower than the ecological carrying capacity, at which population growth rate is zero. In the simplest logistic model, the economic carrying capacity is half of the asymptotic level, K.

These two contrasting definitions, along with those of Leopold (1933) and Errington (1934), illustrate well the variation in uses of the term carrying capacity in wildlife management. This variation largely depends on the management aims and the condition in which the animals or habitat are to be maintained. Dasmann (1964) proposed four definitions based on these distinctions, as well as on the type of factor which limits the population. Conservationists might aim to maintain the highest population density possible in a given area, while game managers would be more concerned with keeping animals in good condition (e.g. Potvin & Huot, 1983). In order for the population to be limited by resources at the ecological carrying capacity, at least some individuals in the population will be in poor condition (Freeland &

Choquenot, 1990), and the standing biomass of vegetation will be reduced to such an extent that it limits the population. The economic carrying capacity is the meaning most often used by range managers and animal production scientists. Under certain circumstances conservationists might also aim to keep a population below its ecological carrying capacity. For example where a national park is to be managed to preserve a diverse array of species, it would be desirable to prevent any one species from reaching a level at which it would deplete other species to levels at which they ceased to be viable (Bell, 1984). Under some circumstances plant-herbivore systems may oscillate quite widely without ever reaching a stable equilibrium (Caughley & Lawton, 1981). In such cases the safest strategy for conservationists might be to maintain the population at lower than maximum levels, to prevent over-exploitation of the habitat and population crashes. This is the basis for the argument that culling may be necessary to maintain relatively high population densities of elephants (Bell, 1984).

In conclusion, Dhondt (1988) recommends that the use of the term be abandoned altogether. However this seems to be a rather drastic solution, as carrying capacity is both meaningful and useful as a general concept. The best use of the term is to refer in general terms to the number of animals that a given area can support over a long period of time, rather than as a precise measure. When using the term, it is therefore necessary to define precisely what is meant by it. In the field of wildlife management, this will generally depend primarily on the management goals.

1.1.2 Approaches to the measurement of carrying capacity

Several different approaches have been taken to estimating carrying capacity (Bell, 1984; Crête, 1989). Firstly, the rate of production of a key resource, usually food or a particular nutrient, can be estimated, and combined with an estimate of the

requirements of an individual of the species concerned to give an estimate of the density of individuals which can be supported. Bell (1984) terms this the analytical approach. Secondly, the response of a population to some perturbation or manipulation can be used with population models to estimate where on the growth curve the population lies, and thus predict the carrying capacity in which ever way it is defined (the manipulative approach). Thirdly, population density can be measured in comparable habitats which are known or thought to be at carrying capacity (the comparative approach).

1.1.2.1 Analytical approach

The analytical approach has been used by several authors studying ungulates. Crête (1989) used such an approach to estimate the carrying capacity for moose (*Alces alces*) in Quebec. This was based on the production of deciduous twigs on which the moose relied during the winter, and corresponded well with the observed density in a protected study site free from hunting (i.e. carrying capacity estimated by the comparative approach), allowing for the fact that there was a net emigration of animals from the area. Potvin & Huot (1983) presented a method for estimating carrying capacity of wintering grounds for white-tailed deer (*Odocoileus virginianus*) managed for hunting. Other examples of the use of the analytical approach to estimate the carrying capacity of ungulates are given in Bell (1984).

Reid *et al.* (1989) used an analytical approach to estimate the change in carrying capacity of Wolong Natural Reserve in China for giant pandas (*Ailuropoda melanoleuca*) following a bamboo flowering and die-off. The panda population exceeded carrying capacity immediately after the die-off, and numbers fell. In simple situations where a small number of foods are involved, as with pandas and bamboo or with moose and deciduous twigs, an analytical approach has proved successful.

Few studies of primates have attempted to estimate carrying capacity. Primates generally live in complex forest habitats and their diets often include a wide variety of food items of varying quality (Chapman & Chapman, 1990), thus making an analytical approach difficult. For example, Coelho *et al.* (1976) estimated from energy requirements and fruit production that a forest in Guatemala could support 8500 individual howler and spider monkeys (*Alouatta villosa* and *Ateles geoffroyi*) per square kilometre, a figure which greatly exceeds the reported population density of any species of non-human primate. This finding was taken to indicate that food resources could never limit the populations. However Cant (1980) pointed out that in fact if the nutritional value of the foods involved is considered, and the estimates of fruit abundance used are reconsidered, that food resources might indeed limit the populations, and thus that the carrying capacity could be much lower.

Problems with the analytical approach include both the difficulty of estimating the production of forage (primary production), and of converting this to the animal biomass which can be sustained (secondary production). Our estimates are unlikely to measure food availability in the same way as an animal. Animals are likely to be more selective than crude sampling techniques, which will tend to overestimate the amount of potential food present (Caughley & Sinclair, 1994). Although models have been extended to include nutritional constraints (Hobbs & Swift, 1985), data on nutritional requirements are unavailable for most wild species and have to be extrapolated from other, usually domestic, species. For example, in order to estimate the nutritional requirements of gorillas, Goodall (1977) was obliged to use data on pigs, the only comparably sized non-ruminant for which data were available. Moreover, the analytical approach also requires that the particular resource which would regulate the population at carrying capacity be known and is greatly complicated if several species utilise the same key resource. Bell (1984) argued that

models relating primary to secondary production, particularly in African ecosystems, are too simplified to allow this approach to be used in all but the simplest situations.

1.1.2.2 Manipulative approach

Fowler & Smith (1973) used a Leslie matrix model to estimate the equilibrium population density and age structure of African elephants (*Loxodonta africana*) populations compressed into restricted areas by habitat loss (i.e. the manipulative approach). The carrying capacity predicted from this model closely matched the known densities before the effects of man. For this, however, data were needed on the population's behaviour at various densities. In harvested populations, if both the level of harvest and the intrinsic rate of natural increase (r_{max} in the logistic equation) can be accurately estimated, ecological carrying capacity can be estimated (Bell, 1984). Caughley (1977) described another method which estimates K and r_{max} from observed changes in population size. However the need for good demographic data and/or knowledge of harvest rates means that these methods are not applicable in all cases, and the carrying capacity estimates will be limited by the quality of the models used. Given the problems inherent in available models (Caughley, 1981), this is a significant limitation.

1.1.2.3 Comparative approach

This is the most straight forward approach to estimating carrying capacity. It depends on the ability to classify habitats in a way which reflects carrying capacity, so that like is compared with like, and on the populations in reference areas being at carrying capacity. Carrying capacity will be underestimated if reference areas are themselves below carrying capacity. However if the aim is a conservative estimate, as might be

the case in a conservation context where the consequences of, for example, overcrowding of elephants would be more deleterious than the consequence of under-populating, then this might be the most appropriate approach.

Grimsdell & Bell (1975; cited in Bell, 1984) used such an approach to estimate the carrying capacity of the Bangweulu floodplain in Zambia for black lechwe. They used the density of lechwe per kilometre of floodline in another site and the length of floodline in the floodplain to produce an estimate of 160,000 lechwe, compared with 185,000 estimated from protein production in the habitat and requirements derived from livestock (i.e. using the analytical approach). In a more sophisticated version of this approach, several studies have established relationships between environmental variables (rainfall and soil nutrient availability) and the observed biomass of ungulates in a cross section of African savanna sites, which can be used to predict carrying capacity of other areas (Coe *et al.*, 1976; Fritz & Duncan, 1994).

A significant advantage of this approach is the fact that it is based on population densities which actually exist. As long as comparable reference areas are available, it is not necessary to identify a particular resource as limiting. If, for example, territorial behaviour limits a population at high densities, this is taken into account by the estimates of population density in reference areas.

In group living species, the population density is a function of both the group size and the density of groups. Group density depends on the sizes of the home ranges of each group, and the degree of territoriality or overlap of these ranges. This suggests an extension of the comparative approach which could be used to estimate carrying capacity, based on not only the observed population density in reference areas, but the use of habitats in those areas, that is on the relationships between habitat quality, group size and home range size. This is the approach taken to estimating the carrying capacity of the Virungas for mountain gorillas in this study.

1.2 THE VIRUNGA GORILLA POPULATION

The mountain gorilla is the rarest of the three subspecies of gorilla and exists in just two small isolated populations in the Virunga Volcanoes on the borders of Rwanda, Zaire and Uganda (Figure 1.1) and in the Impenetrable forest in Uganda. This thesis is concerned with the Virunga population. The forested area of the Virungas covers approximately 440 km^2 and includes an altitudinal range from 2000 m in the lowest sections on the Zairean side to 4500 m at the summit of Mount Karisimbi. It is protected as contiguous national parks in each of the three countries but is completely isolated by human habitation and cultivation. Annual rainfall is around 2000 mm, with a bimodal pattern (Plumptre, 1991). March to May and September to November are wet seasons, while June to August and December to February are drier. However the pattern is variable and little evidence of seasonal variation in the biomass and growth rate of plants has been found (Plumptre, 1991).

1.2.1 Conservation history

The Virunga population was first studied in 1960 by George Schaller, who estimated that there were 400-500 individuals at that time (Schaller, 1963). During the 1960s and 1970s the population declined dramatically to just 250 by 1981 (Harcourt *et al.*, 1983; Aveling & Harcourt, 1984; see Figure 1.2). This decline can be attributed to a combination of factors (Weber & Vedder, 1983). Some 40 % of the Rwandan section was converted to agricultural use in 1968-69 as part of a European funded scheme to grow pyrethrum as a cash crop. However the majority of the decline occurred in the region of Mount Mikeno in Zaire, where direct hunting was likely to have been prevalent during the civil war in Zaire in the mid-1960s. During the 1970s markets developed for gorilla trophies, primarily skulls and hands, and for live young. It is unknown how many gorillas were killed to satisfy this trade, but there were at least

Figure 1.1. Map of the Virunga volcanoes showing the international and national park boundaries, the location of Karisoke Research centre and the approximate boundaries of the Karisoke study site. Contours are at 100 m intervals, the highest point being the summit of Mount Karisimbi at 4507 m.

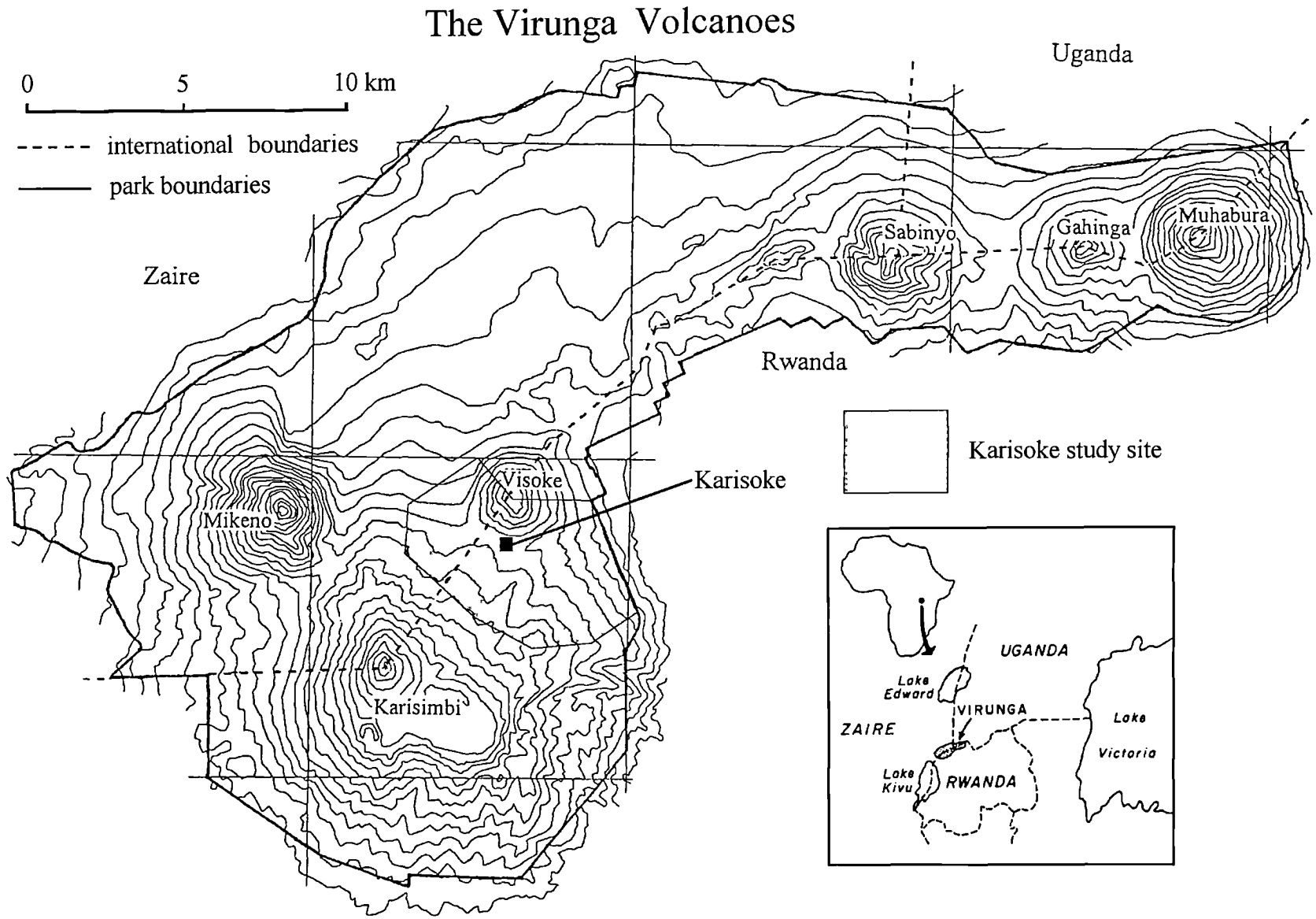
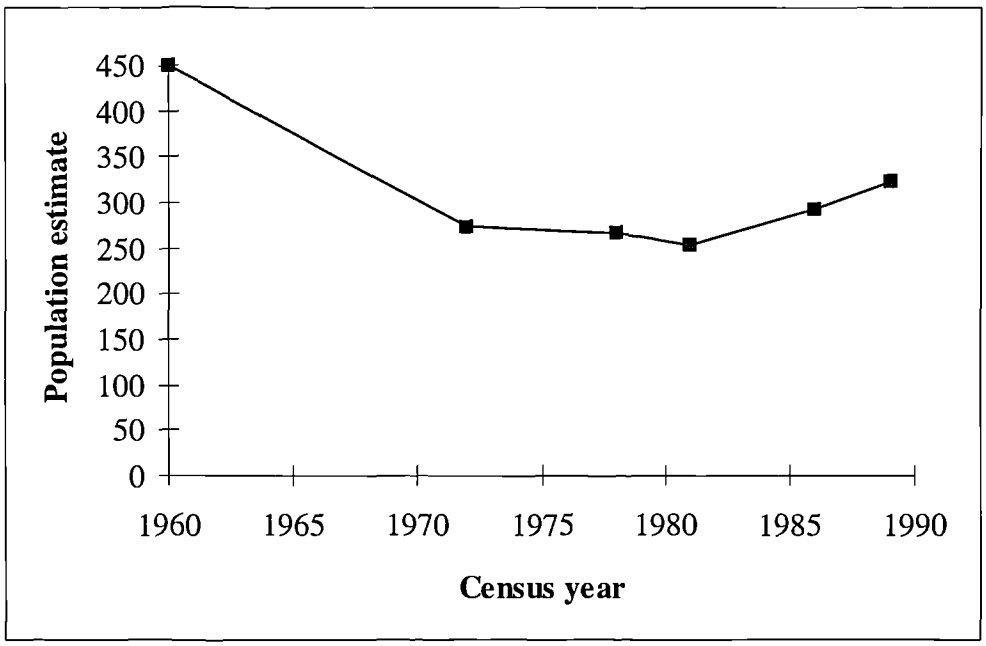

The Virunga Volcanoes
0
5
10 km
international boundaries
park boundaries
Uganda
Zaire
Rwanda
Sabinyo
Gahinga
Muhabura
Visoke
Karisoke
Mikeno
Karisimbi
Karisoke study site
UGANDA
Lake Edward
VIRUNGA
ZAIRE
Lake Victoria
Lake Kivu
RWANDA

Figure 1.2. Changes in the size of the Virunga population of mountain gorillas, 1960-1990. See text for data sources.



13 in known groups and possibly many more (Harcourt & Fossey, 1981). Other forms of human disturbance which could have contributed to the decline include illegal cattle grazing within the park and poaching of antelope using snares in which gorillas can be caught (Harcourt & Fossey, 1981; Aveling & Harcourt, 1984).

In response to this macabre trade and the resulting publicity, the Mountain Gorilla Project was set in up in 1979 in Rwanda by a consortium of international organisations (Harcourt, 1986). The first approach of this three-pronged project was to improve park security. Guard numbers were increased and their training and equipment improved. Secondly, a conservation awareness programme was initiated, targeting all levels of the human population, particularly in the area around the park. Thirdly, a controlled ecotourism programme based on gorilla viewing was started as a means of generating income for the park. A similar project was launched in the Zairean section of the forest in 1984 (Aveling & Aveling, 1989). With the improved protection afforded by these two projects, the population decline was halted by 1986 (Aveling & Aveling, 1989) and by 1989, when the most recent census was made, the population had increased to an estimated 324 individuals (Sholley, 1991), as shown in Figure 1.2.

1.2.2 Previous studies

Since 1967 mountain gorillas have been studied in the section of the Virungas around the Karisoke Research Centre (Figure 1.1). Gorillas have been found to live in groups of 2 to over 20 individuals, generally consisting of one or two mature adult males, with a number of adult females and immatures (Harcourt *et al.*, 1981; Yamagiwa, 1987). Both males and females may leave their natal group, females transferring to other groups and males ranging as lone silverbacks (Harcourt *et al.*, 1976). Mountain gorilla diet, movement patterns and habitat use have been

extensively studied in the Karisoke study area (Fossey, 1974; Fossey & Harcourt, 1977; Watts, 1984, 1991; Vedder, 1984). A recent study on plant-herbivore dynamics and competition among the five large herbivores in the Karisoke study site, including mountain gorillas, found that elephants were most likely to affect the food supply of the gorillas, but were present in such low numbers as to be unlikely to have a major impact (Plumptre, 1991). Although food availability has been shown to be the main determinant of gorilla ranging patterns (Vedder, 1984; Watts, 1991), Plumptre (1991, 1995) found that food was unlikely to be limiting the population.

However, little is known about the ecology of the gorillas in other parts of the Virungas and several lines of evidence suggest that there may be differences elsewhere. The altitudinal range of the Karisoke study site (2800 to 3600 m) covers only around half of the range occupied by gorillas, which are found down to the lowest parts of the forested area on the Zairean side. Vegetation types in tropical montane regions such as the Virungas vary considerably with altitude (Lebrun, 1960a, 1960b; Spinage, 1972; White, 1981) and available vegetation maps indicate that different types exist in areas outside the Karisoke study site (Marius, 1976). Each survey made of the population has found considerable variation in gorilla density in different areas (Schaller, 1963; Harcourt & Fossey, 1981; Weber & Vedder, 1983; Aveling & Harcourt, 1984; Aveling & Aveling, 1989; Sholley, 1991). Several authors have noted a difference in group size as well as population density between the eastern section of the Virungas (Mounts Sabinyo, Gahinga and Muhavura) and the remainder (Harcourt *et al.*, 1981; Harcourt & Fossey, 1981; Weber & Vedder, 1983). Harcourt & Fossey (1981) suggested that differences in the level of human disturbance between different areas could account for this variation, while Weber & Vedder (1983) indicated that differences in habitat were more likely to be the primary cause.

On the basis of observed patterns of habitat use by gorillas in the Karisoke study site, Weber & Vedder (1983) divided the Virungas into areas considered as potential year round habitat, habitat usable only seasonally or by extremely low numbers of gorillas and habitat virtually unusable by gorillas. However in recent censuses (Sholley, 1991; A. Vedder, *pers. comm.*) and in the development of tourism projects (C.R. Sholley and R. Aveling, *pers. comm.*), gorilla groups have been found in both of the second two habitat classes. Clearly the gorillas are able to use a wider range of habitats than was previously thought. As mentioned above, the gorilla population was found to be increasing at the most recent census (Sholley, 1991). Given the loss in habitat since the first estimates of the population size were made (Schaller, 1963), and the poor understanding of the habitat requirements of gorillas, it is not known how far the population could continue to rise.

1.2.3 Aims of this study and justification of the approach taken

The overall aims of this study were fourfold. Firstly it aimed to map the availability of vegetation types, as potential gorilla habitat, across the whole protected forested area of the Virungas, and to estimate the quality of these habitats in terms of the availability of gorilla foods in each. Secondly, it aimed to investigate the variation in gorilla ranging behaviour, habitat utilisation and diet across a wider range of habitats than those found and previously studied in the Karisoke study site. Thirdly, it aimed to investigate the effects of human disturbance on the population. Lastly, it aimed to obtain an estimate of the carrying capacity of the Virungas for gorillas, based on the availability of habitat and the current patterns of habitat use.

The approach taken to estimating carrying capacity is thus a modification of the comparative approach described by Bell (1984). Given the complex mosaic of habitats in the Virungas, the lack of understanding of what limits the population and

the problems associated with either of the other approaches described above, this is the best approach. Basing estimates on not only the population density found in reference areas, but also the patterns of ranging and habitat use there, should provide realistic estimates of carrying capacity. The aim in this study is to obtain a conservative estimate of carrying capacity, that is of how many gorillas the Virungas could support, assuming current patterns of habitat use are maintained and by implication without significant reductions in the condition of the population or degradation of the habitat. The underlying assumption is that the resources available per individual would not be reduced if the relationships between group size, food density and home range size observed among the study groups were maintained.

In October 1990, four months after the start of fieldwork on this project, a rebel force, made up mainly of Rwandan refugees based in Uganda, invaded the north-eastern part of Rwanda and all expatriate workers in the Virungas were forced to leave the country. Fighting reached the Virunga area by January 1991, particularly in the eastern section forming the border with Uganda, which was mined and frequently shelled. Although it was possible to return to Karisoke by March of that year, it was not possible to continue work in the eastern section. In addition the rebels periodically used parts of the central saddle region between Mounts Sabinyo and Visoke to mount attacks on the local area, and access to this area was often restricted. In February 1993, shortly before fieldwork on the project was due to finish, the rebels launched a major attack, taking almost all of the Virunga region, and expatriates were again evacuated. It was not therefore possible to sample vegetation and gorilla habitat use in as wide a range of areas as intended. However the data collected, along with information from aerial photographs and the limited fieldwork done before the war, did enable an overview to be obtained of the habitats and their use in the Virungas.

1.3 THESIS PLAN

In Chapter 2 a classification of habitat types within the Virungas is described, a habitat map is presented and the overall availability of these habitats is measured. The availability and distribution of gorilla foods within each habitat are investigated.

Chapter 3 investigates the patterns of use of the available habitats by gorilla groups. An overview of six groups monitored by trackers and guides is given, and the relationships between group size, home range size and food density are investigated. The patterns of habitat selection within the home ranges of two groups are investigated in more detail.

The diets of two groups occupying contrasting habitats are examined in Chapter 4. The responses of the two groups to different levels of food availability are compared, in terms of dietary diversity and selection. The accuracy of different methods of measuring dietary intake are compared.

Chapter 5 investigates the effects of human disturbance on the gorilla population. Data on the distribution of gorilla groups and illegal use (poachers' snares) from the most recent census are presented, and the relationships between signs of illegal human use, snare density and signs of gorilla use, surveyed at a sample of sites across the Virungas, are investigated.

Chapter 6 uses the information on the availability of habitats and their use by gorillas presented in previous chapters to make estimates of the number of gorillas that the area could support, using several different methods. The value and management implications of these estimates are discussed.

CHAPTER TWO

THE AVAILABILITY AND QUALITY OF HABITATS IN THE VIRUNGAS

2.1 INTRODUCTION

An understanding of the distribution and abundance of resources is fundamental in any study attempting to understand the factors influencing population density and patterns of habitat utilisation. In the case of mountain gorillas, food is likely to be one of the most important, if not the most important resource. Gorillas in the Virungas appear to be able to use any area with herbaceous vegetation as nesting sites and very rarely drink water (Schaller, 1963; Fossey, 1974, 1983). Cover is abundant virtually everywhere and predation by leopards, the only non-human predator, has not been recorded since 1961 (Tobias, 1961; Schaller, 1963).

Previous studies of the Virungas ecosystem have identified a large scale pattern of distinct vegetation types, with much of the variation being attributable to changes in altitude (Lebrun, 1960a, 1960b; Schaller, 1963; Spinage, 1972; Fossey & Harcourt, 1977). The vegetation in parts of the Virungas was mapped by Marius (1976), who identified 14 vegetation types. These maps, however, do not cover large parts of the Zairean side of the forest and lump together certain areas under one category where the vegetation is quite different on the ground. For instance the term secondary forest is used to describe both open herbaceous areas on the sides of Mount Visoke, and mixed forest at considerably lower altitudes to the west of Mount Mikeno (*personal observation*).

The availability and distribution of gorilla food plants has previously been investigated in some detail in the study site around the Karisoke Research Centre.

Watts (1983, 1984), who measured gorilla food availability specifically, found that food was generally both abundant and ubiquitous, but that food species generally showed a clumped distribution. Considerable variation was found in both the richness (number of food species) and the abundance of food between habitat types. Plumptre (1991) also found heterogeneity in the composition of the vegetation both between and within habitats. He found that the total biomass of herbaceous plants and the species richness per habitat decreased with altitude. Diversity, however, increased as the evenness of species was greater at higher altitudes, whereas at lower altitudes a few species tended to dominate. Neither study found evidence of seasonality in the general patterns of food availability, with the exception of bamboo (*Arundinaria alpina*) shoots which only appear at certain, generally wetter, times of year.

Although the area around Karisoke has been well studied, the vegetation in other areas of the forest, particularly at lower altitudes, is quite different and might be expected to contain different potential foods with different patterns of distribution and abundance. As mentioned in Chapter 1, earlier studies have labelled as poor gorilla habitat (Weber & Vedder, 1983) areas in which recent censuses have found several groups of gorillas (Sholley, 1991; Aveling & Aveling, 1989). In considering the conservation of the population it is clearly important to have a complete picture of the availability and quality of habitats for the gorillas across the whole area. The aims of this part of the study were to map the overall pattern of habitats across the whole range of the Virungas and measure the availability and distribution of food resources within each.

2.2 METHODS

2.2.1 Classification of habitat types

A classification of nine habitat types was established based on those used by Watts (1983) and Plumptre (1991), simplified slightly and extended to include types found in parts of the Virungas away from the Karisoke study area. The classification has an element of subjectivity, but the differences between habitat types are quite obvious on the ground and previous studies have found considerable differences in the vegetation between habitat types based on similar distinctions (Watts, 1983; Plumptre 1991). The classification chosen allowed each type to be distinguished on aerial photographs. Some previous authors have used the term vegetation zone, but habitat type is used here following Plumptre (1991, 1994) and because they are considered primarily as potential habitats for the gorilla population. The nine habitat types were as follows (altitudinal ranges are approximate):

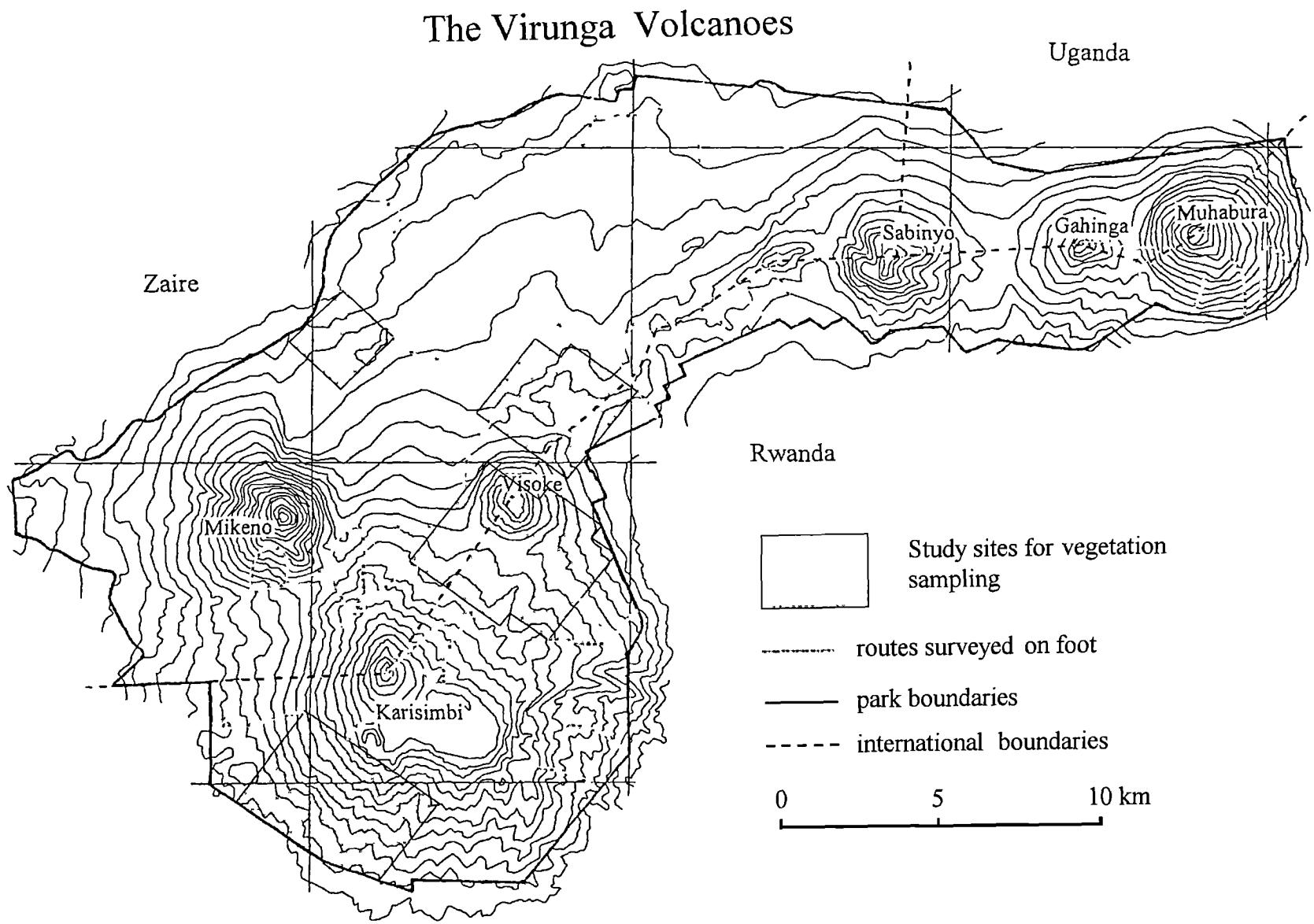
1. **Alpine** (above 3600 m). Areas above the limit of most herbaceous and woody plants, with low grass and mosses and occasional *Senecio johnstonii*. Bare rocky areas, especially on top of Mounts Mikeno and Sabinyo were also included as Alpine.
2. **Subalpine** (3300 m to 3600 m). High altitude vegetation, up to 4-5 m high, with abundant *Senecio johnstonii*, *Lobelia stuhlmanni* and/or *L. wollostonii*, *Hypericum revolutum* and *Rubus kirungensis*.
3. **Brush Ridge** (2950 m to 3300 m). Dense vegetation along the ridges and ravines on the sides of the volcanoes, with abundant *Hypericum revolutum* and shrubby growth of *Senecio mariettae*, reaching around 10 m high.
4. **Herbaceous** (2800 m to 3300 m). Open areas with low (1-2 m), dense herbaceous vegetation, generally on the sides of volcanoes, with very few *Hagenia abyssinica* and *Hypericum revolutum* trees.

5. ***Hagenia*** (2750 m to 3300 m). Equivalent to the 'Saddle' zone of previous authors, a variable canopy woodland dominated by *Hagenia abyssinica* and *Hypericum revolutum* trees reaching up to 20 m, with a dense herbaceous or, less frequently, grassy understorey found in the saddles between certain volcanoes and on the less steep lower slopes.
6. **Bamboo** (2550 m to 2950 m). Areas dominated by often monospecific stands of bamboo (generally 5-12 m high), mixed with a few trees and vines at lower altitudes.
7. ***Mimulopsis*** (2550 m to 2800 m). Open herbaceous areas, differing from the Herbaceous zone in being found at lower altitudes, generally in the flat saddle between Visoke and Sabinyo and often dominated by *Mimulopsis excellens.*
8. **Mixed Forest** (2000 m to 2550 m). A mixed species montane forest, with abundant *Neobutonia macrocalyx* and *Dombeya goetzenii.* Other tree species include *Bersama abyssinica, Croton macrostachys, Clausena anisata, Maytenus heterophylla, Maesa lanceolata, Pygeum africanum* and *Tabernaemontana johnstonii.* The open canopy reached up to 20 m high and the understorey consisted of herbaceous vegetation, with dense patches of *Mimulopsis arborescens.*
9. **Meadow**. This term was used to describe open grassy areas at a variety of altitudes. These areas were often marshy and contained very little gorilla food. A large area on the east side of Muhavura which was reported as dry and shrubby and which burned extensively in 1989, was included as Meadow.

2.2.2 Preparation of habitat map

In addition to the sites in which vegetation was sampled as described below, survey routes were walked in other areas of the Virungas as shown in Figure 2.1 and notes were made on the composition of the vegetation in each. Information on the

Figure 2.1. The location of study sites where vegetation was sampled and routes surveyed on foot for vegetation ground-truthing in the course of the habitat mapping.


The Virunga Volcanoes
Uganda
Zaire
Rwanda
Sabinyo
Gahinga
Muhabura
Visoke
Mikeno
Karisimbi
Study sites for vegetation sampling
routes surveyed on foot
park boundaries
international boundaries
0
5
10 km

character of the vegetation elsewhere was obtained from park guards and other researchers working in the area. Using this personal experience of the area, the habitat types were identified on a series of 1:50 000 aerial photographs taken in 1990 by the Institut Géographique National, Paris. The zones were then outlined on a 1:100 000 topographic map using a zoom transfer scope at the Cook County Centre for Remote Sensing and Spatial Analysis of Rutgers University, New Jersey, USA. The polygons outlining each patch of each type of habitat were digitised into the Geographic Information System (GIS) set up by that organisation of the Virunga area using GRASS 4.1 software. This system was then used to produce a map of the habitat types, and to calculate the total area of each. The slope on the steeper sides of the volcanoes would have added around 15 % to the areas, by simple geometry. However, on these slopes a certain, indeterminate proportion of the ground was not reachable by the gorillas, for example on the sides of ravines. No attempt was therefore made to correct areas for slope.

2.2.3 Vegetation surveys

In order to estimate the mean biomass of gorilla food plants in each habitat type, vegetation surveys were made in a representative range of study sites across the Virungas (Figure 2.1). An overall list was compiled of food plants observed or reliably reported to be eaten by the gorillas anywhere in the Virungas in the course of collecting the data on diet described in Chapter 4. Plants were identified using the Karisoke Research Centre herbarium, Troupin (1977-1988) and at the herbarium of the Institut de Recherche Scientifique et Technique, Butare, Rwanda. Plant names throughout this thesis follow Troupin (1977-1988).

In each study site, gorilla food plants were sampled using a stratified random technique (Grieg-Smith, 1983). A baseline was measured and marked across the

middle of each site, and used to establish a grid system. In the majority of vegetation types a grid with cells of 500 m x 500 m was used, with 200 m x 200 m cells where the larger grid would not have yielded a sufficient number of sample points. Vegetation was measured at one random sampling point within each grid cell, the location of which was determined from random number tables and arrived at by pacing. Pace size was checked regularly along measured stretches of 50 m in typical terrain. A total of 405 points were sampled, between June, 1992 and February, 1993. The biomass of each food was estimated in concentric, circular, sample plots, centred on each sampling point and varying in area as follows.

1 m^2 All herbaceous plants were counted and the length of each stem measured. The wet weights of *Galium* spp. and of leaves of other vines were measured in the field.

10 m^2 The length and circumference of stems of *Lobelia* spp. and the lengths of stems of *Rubus* spp. were measured. The number of bamboo stems and, during the bamboo shooting season, the number of shoots were counted.

100 m^2 All species of tree were counted. For those species from which the gorillas ate the pith of stems, the total length of stem of suitable size was estimated.

The dry biomass of each gorilla food in each plot was estimated from these data in a variety of ways. Samples of *Galium* and of leaves of other vines were collected, dried and reweighed in order to estimate the mean water content and thus the dry biomass in each plot. Stems of herbaceous plants and pith from the branches of woody plants were estimated by collecting measured lengths. These samples were prepared using techniques comparable to those of feeding gorillas, then dried and weighed to estimate the dry biomass of food per metre of stem. The area of the internal surface of hollow stems of *Lobelia* and thus the volume of pith were estimated from the external dimensions and converted to dry biomass in a similar way. Plumptre (1991) calculated regression equations relating the dry biomass of leaf

to stem length for many herbaceous species. These equations were used to estimate dry biomass of leaf for several species. One further equation was calculated in the same way for *Boehmeria platyphylla* which was not present in Plumptre's study area. The equations used are given in Appendix 1. For bamboo shoots and roots of *Carduus* spp., the mean biomass eaten per plant was calculated from the observations of feeding in one group of gorillas described in Chapter 4. This was multiplied by the number of plants or shoots in each plot. Only *Carduus* plants over 1 m high, which was the approximate lower size limit of plants from which the gorillas ate roots, were included. Roots from a sample of *Piper capense* plants, which gorillas ate whole, were dried and weighed to estimate the mean biomass per plant. All samples were dried in paper bags suspended over a charcoal burning stove until no further reduction in weight was detected.

The mean biomass of each food in habitat type, except Meadow and Alpine, was calculated from the estimated biomass in each plot in that habitat. Meadow and Alpine contain virtually no gorilla food and are virtually never used by them. The biomass of bamboo shoots was calculated using only those plots measured in Bamboo during the shooting season (30 plots out of a total of 60). It was estimated from the Karisoke Research Centre trackers' daily reports from 1988 to 1992 that bamboo shoots were available for an average of three months per year. The biomass estimate was therefore multiplied by 0.25, to give an estimate of mean annual availability.

2.3 RESULTS

The habitat map of the Virunga area is shown in Figure 2.2, and the total area of each habitat type is given in Table 2.1. The total area of 442 km^2 measured is slightly larger than previously published estimates (420 km^2, Weber & Vedder, 1983). The difference however, is only 5 % and the overall pattern of habitat types is unlikely to

Figure 2.2. The habitat map of the Virunga volcanoes produced from aerial photographs and ground truthing as described in the text.

Habitat Types in the Virungas

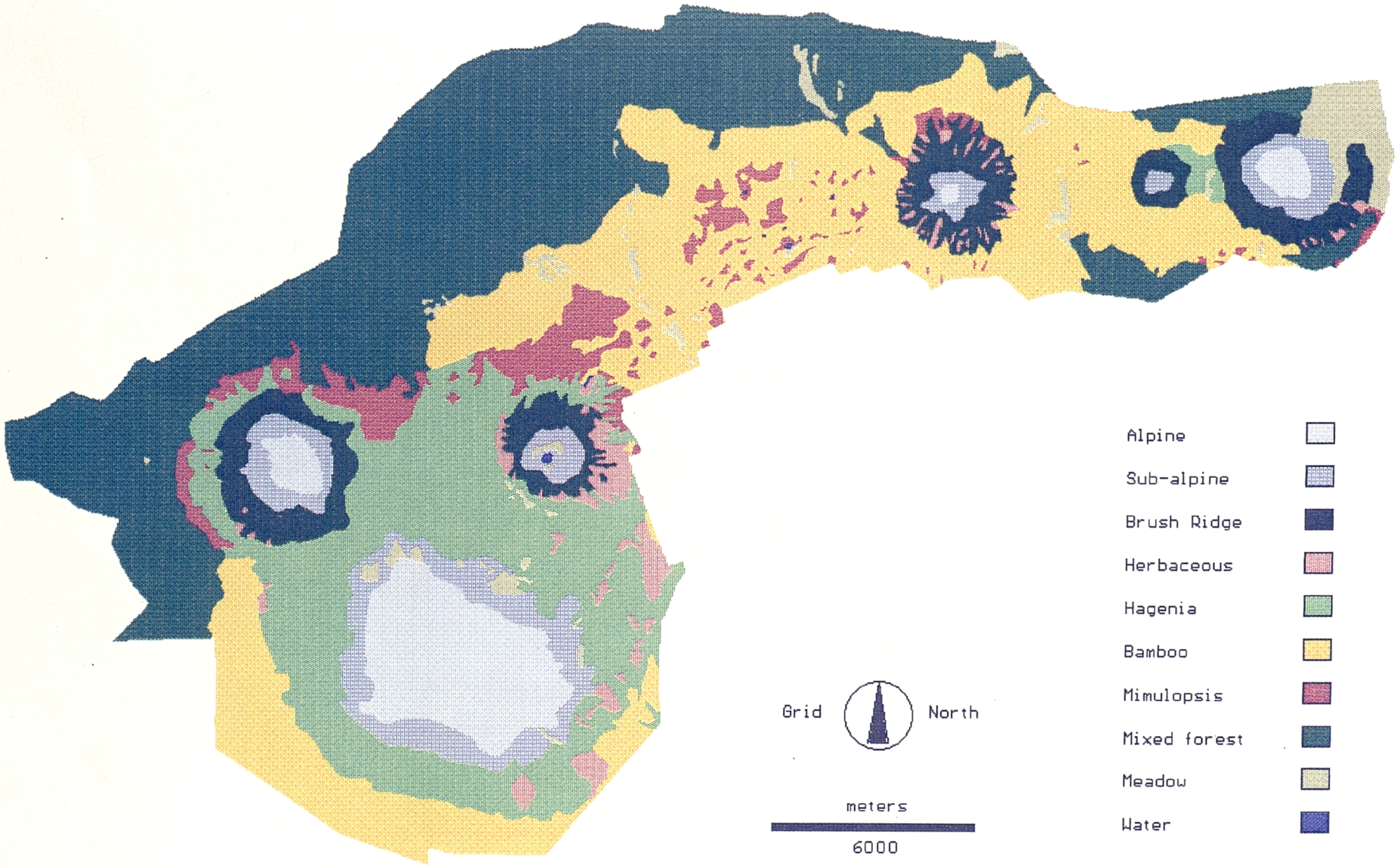


Table 2.1. The areas and percentages of the total area of each habitat type within the Virungas protected forested area, calculated from the habitat map shown in Figure 2.2 and described in the text.

Habitat	**Area (km^2)**	**Percentage**
Alpine	26.8	6.0
Subalpine	25.2	5.7
Brush Ridge	29.6	6.7
Herbaceous	9.4	2.1
Hagenia	72.6	16.4
Bamboo	113.2	25.6
Mimulopsis	20.5	4.6
Mixed Forest	133.0	30.1
Meadow	11.8	2.7
Open water	0.2	0.1
Total	442.3	100.0

be greatly affected. There could be errors in either estimate as no accurate maps of the area exist. The figure obtained in the current study agrees more closely with that of Weber & Vedder (1983) than with the figure of 375 km^2 quoted by Harcourt & Fossey (1981).

The majority of the region is covered by three major types, Mixed Forest in the lower altitude areas, chiefly on the northern, Zairean side of the range; Bamboo between the volcanoes in the central and eastern sections with a broad strip at the southern end of the range; and *Hagenia* forest in the higher plateau around the volcanoes in the western section. These three habitats together make up 72 % of the whole area. The slopes of the volcanoes are generally covered by Brush Ridge, Subalpine and Alpine vegetation. Unfortunately the state of development of the Virunga GIS system did not allow the habitat map to be superimposed on a topographic map, but these habitat types do represent an altitudinal zonation. Distributed through this pattern are patches of open herbaceous vegetation (Herbaceous and *Mimulopsis*) and Meadow.

Considerable variation was found in the gorilla foods occurring in these different habitats (Table 2.2). A few foods species or genera such as *Galium* and *Laportea alatipes* were fairly ubiquitous, but the majority occur in a small number of habitats. The commonest foods overall include *Peucedanum linderi*, *Laportea* and *Carduus* (all tall herbs) and the vines *Galium* and *Urera hypselodendron.* Most of these species were recorded as common food items by Watts (1984). The biomass of bamboo shoots during the shooting season was estimated as 2.11 g/m^2, but being available during on average only 3 months per year the effective mean biomass was low.

Table 2.3 gives various indices of habitat quality for each habitat type. The total biomass of food varied considerably between habitats. Herbaceous foods, which are the most important foods in the gorillas' diets (Watts, 1984 and see Chapter 4) made

Table 2.2. Estimates of the mean biomass of gorilla food species in each habitat type, excluding Alpine and Meadow which are very rarely used by gorillas and contain virtually no gorilla food. Units are grams dry weight per m^2 of the plant part eaten (sh = shoots, lf = leaf, st = stem, pi = pith, ls = leaf and stem together, rt = root, lb = leaf base). Standard deviations are given in parentheses.

Species	Part	Subalpine	Brush ridge	Herbaceous	*Hagenia*	Bamboo	*Mimulopsis*	Mixed forest
Arundinaria alpina	sh					0.53 (0.62)		
Acalypha psilostachyaa	lf							0.50 (1.34)
Basella alba	lf					0.01 (0.04)	0.26 (0.77)	0.14 (0.49)
Boehmeria platyphylla	lf							2.09 (4.27)
Boehmeria platyphylla	st							2.91 (5.72)
Cinereria deltoidea	lf			0.19 (1.33)	1.65 (5.83)		0.52 (1.91)	
Carex bequaertii	lb			0.06 (0.48)				
Carduus leptocanthus	lf						0.03 (0.27)	
Carduus nyassanus	lf	7.71 (19.34)	6.06 (9.42)	8.82 (19.46)	7.36 (25.23)			
Carduus nyassanus	rt	2.33 (6.74)		2.00 (7.26)	2.39 (11.14)			
Carduus nyassanus	st	3.09 (7.51)	0.66 (1.44)	1.73 (6.18)	2.70 (11.59)			
Clematis simensis	lf		0.15 (0.48)	0.03 (0.22)	0.06 (0.56)	0.03 (0.221)	0.16 (0.75)	0.16 (0.78)
Clematis simensis	st							0.39 (3.56)

Table 2.2, continued.

Species	Part	Subalpine	Brush ridge	Herbaceous	*Hagenia*	Bamboo	*Mimulopsis*	Mixed forest
Cyperus mannii	lb				0.31 (2.09)			
Cyperus mannii	lf				5.60 (30.84)			
Droguetia iners	lf			0.36 (0.99)	0.14 (0.66)		0.97 (1.75)	1.32 (2.78)
Discopodium penninervium	pi			0.26 (0.58)	0.03 (0.174)		0.77 (0.77)	
Gynura scandens	lf							0.02 (0.16)
Galium spp.	ls	11.64 (36.44)	2.61 (5.83)	3.44 (6.47)	6.42 (16.94)	0.07 (0.53)	1.68 (3.39)	1.80 (6.46)
Iponea involucrata	lf							0.59 (1.72)
Laportea alatipes	lf		1.12 (2.04)	7.62 (9.38)	8.11 (19.07)	0.72 (2.13)	0.09 (0.75)	0.06 (0.43)
Laportea alatipes	st		4.06 (7.30)	30.17 (38.00)	32.12 (75.10)	2.68 (8.23)	0.34 (2.76)	0.23 (1.60)
Lactua attenuata	lf						0.02 (0.14)	0.02 (0.22)
Lobelia stuhlmanii	pi	3.93 (10.19)	0.76 (2.39)					
Mimulopsis arborscens	pi							0.65 (1.00)
Mikania capensis	lf				0.05 (0.42)	0.14 (0.63)	2.70 (6.86)	0.89 (1.89)
Momordica pterocarpa	lf							0.65 (1.80)
Mikaniopsis clematoides	lf					0.01 (0.03)		0.09 (0.56)

Table 2.2, continued.

Species	Part	Subalpine	Brush ridge	Herbaceous	*Hagenia*	Bamboo	*Mimulopsis*	Mixed forest
Oreosyce africana	lf				0.12 (1.09)	0.03 (0.25)	0.05 (0.44)	0.44 (1.23)
Piper capense	rt							0.27 (1.20)
Peucedanum linderi	st			12.85 (19.69)	3.99 (24.18)	0.45 (3.47)	0.16 (1.30)	
Prenanthes subpeltata	lf				0.02 (0.17)			
Rumex ruwenzoriensis	st	0.21 (1.02)			0.51 (2.78)			
Rubus spp.	lf	0.04 (0.20)	0.73 (2.32)		1.24 (7.37)		0.31 (1.82)	0.14 (1.27)
Senecio johnstonii	pi	8.74 (10.21)	0.50 (1.58)		0.48 (2.314)			
Tinospora caffra	lf		0.73 (1.91)		0.09 (0.56)			
Taccazea apiculata	lf							0.18 (1.13)
Taccazea apiculata	st							1.04 (5.16)
Urera hypselodendron	lf					0.01 (0.05)	0.56 (2.80)	2.13 (3.74)
Urera hypselodendron	st					0.02 (0.17)	1.05 (5.82)	3.33 (6.79)
Urtica massaica	lf			2.94 (10.47)	0.94 (5.94)		3.84 (8.26)	
Urtica massaica	st			4.33 (15.16)	1.41 (8.86)		5.46 (11.63)	
Vernonia auriculifera	pi					0.05 (0.25)	0.20 (0.58)	0.76 (0.88)

Table 2.2, continued.

Species	Part	Subalpine	Brush ridge	Herbaceous	*Hagenia*	Bamboo	*Mimulopsis*	Mixed forest
Vine sp. A	lf						0.09 (0.54)	
Vine sp. A	st						0.07 (0.41)	
Vernonia adolfi-fredricii	pi			0.02 (0.075)	0.06 (0.48)			
Vernonia sp.	lf						0.66 (1.82)	

Table 2.3. Parameters of gorilla food availability and distribution for each of the main habitat types.

	Subalpine	**Brush ridge**	**Herbaceous**	***Hagenia***	**Bamboo**	***Mimulopsis***	**Mixed forest**
Number of plots	24	10	70	88	60	68	85
Mean altitude of plots	3460	3210	3060	3130	2790	2710	2280
Biomass of all foods g/m^2	37.7	17.4	74.9	76.0	4.2 (6.3)	20.1	20.9
Biomass of herbaceous foods g/m^2	25.0	15.4	74.6	74.1	4.2	18.8	19.3
Percentage of plots containing food[b]	58	80	100	92	28	93	88
Mean number of food species[b] per plot	0.7	1.6	2.4	1.7	0.4	2.0	2.6
Richness (number of food species in habitat)	6	8	13	20	11 (12)	20	23
Diversity of foods in habitat (Shannon-Wiener index)	1.67	1.83	1.85	2.03	1.19 (1.43)	2.32	2.75

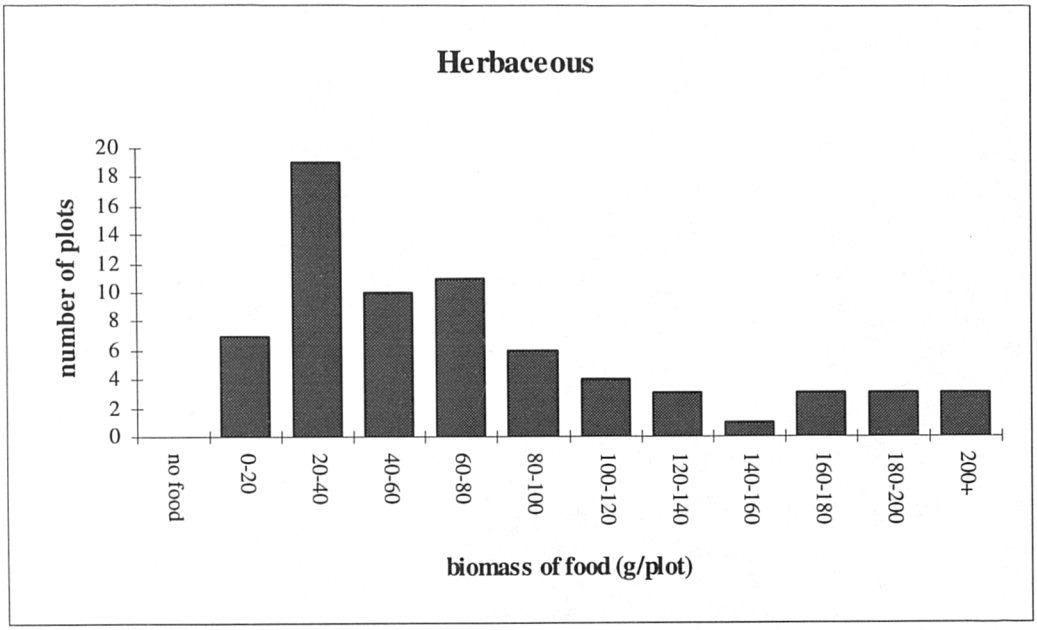
[a] Figures in parentheses include bamboo (*Arundinaria alpina*) shoots and apply to the shooting season only.
[b] Calculated from herbaceous foods only (see text).

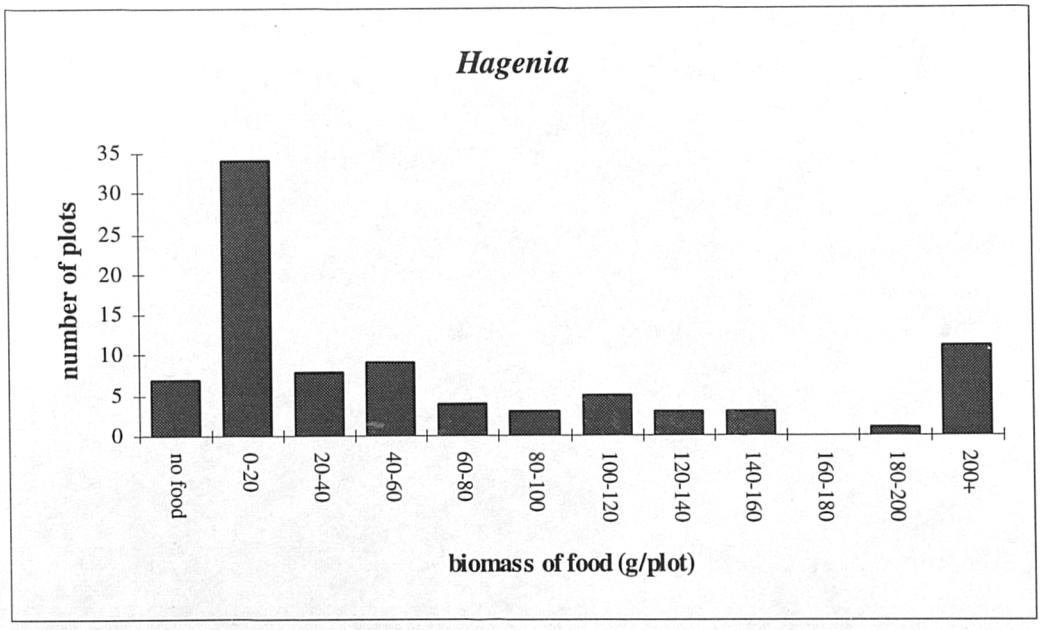
up almost all of the total biomass in all habitats except Subalpine, where pith from the woody branches of *Senecio johnstonii* was relatively abundant. The biomass of herbaceous foods was estimated in a consistent way within 1 m^2 plots, allowing statistical analyses. These data were not normally distributed, so nonparametric tests were used. The variation in the biomass of herbaceous foods between habitat types was found to be highly significant (Kruskal-Wallis, $H = 152$, $d.f. = 6$, $p < 0.001$). Nonparametric multiple comparisons (Dunn, 1964; cited in Zar, 1984) indicated that Herbaceous contained a higher biomass of food than any other habitat, that *Hagenia* contained more than three of the others, and that the biomass was lower in Bamboo than all other habitats except Subalpine and Brush Ridge (Table 2.4). Only one significant difference was found between Brush Ridge and any other habitat, probably because of the small number of plots sampled there.

Despite the variation in the total biomass of food between habitats, the overall frequency of food, that is the percentage of plots containing some herbaceous food, was high (above 80%) in all habitats except Subalpine and Bamboo (Table 2.3). However considerable variation was found in the biomass of herbaceous food at individual sampling points within each habitat. Figure 2.3 shows histograms of the frequency of plots containing different biomasses of herbaceous foods. The majority of plots in most habitats contained relatively small amounts of food, while a few contained considerably more. The large variation in the biomass per plot suggests a clumped distribution of food, particularly in the Herbaceous and *Hagenia* habitats. Less variation was found in *Mimulopsis* and Mixed Forest, suggesting a more evenly distributed pattern of food availability. A large proportion of plots in Subalpine and particularly in Bamboo contained no herbaceous food at all, indicating a sparse distribution.

The mean number of food species per plot varied between 0.7 in Subalpine and 2.6 in Mixed Forest (Table 2.3). The variation between habitats was found to be highly

Figure 2.3. The frequency of plots containing different biomasses of herbaceous foods in each habitat type, except Brush Ridge where only ten plots were sampled.





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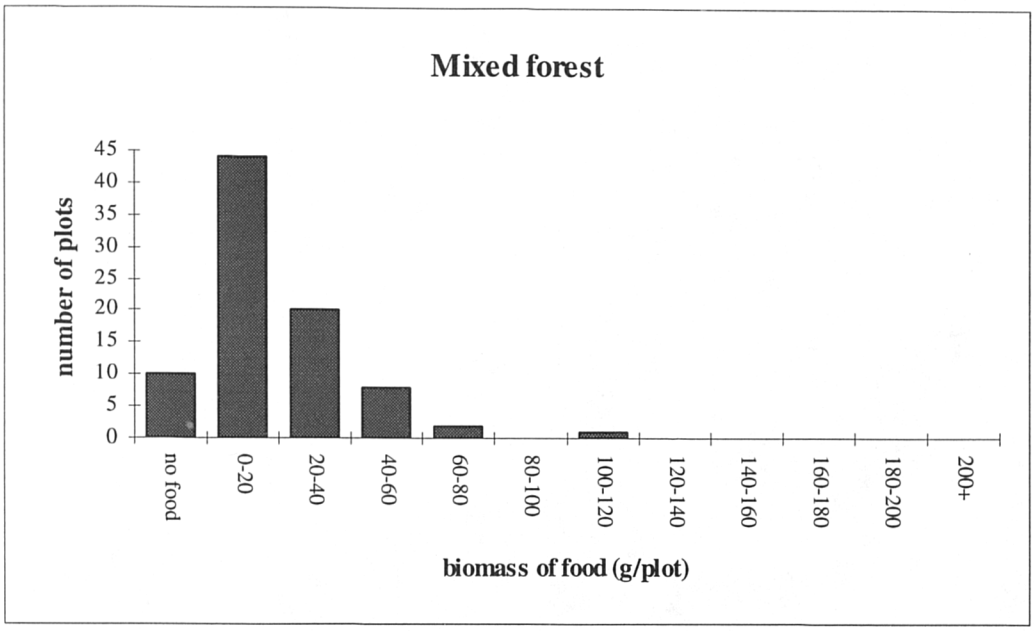

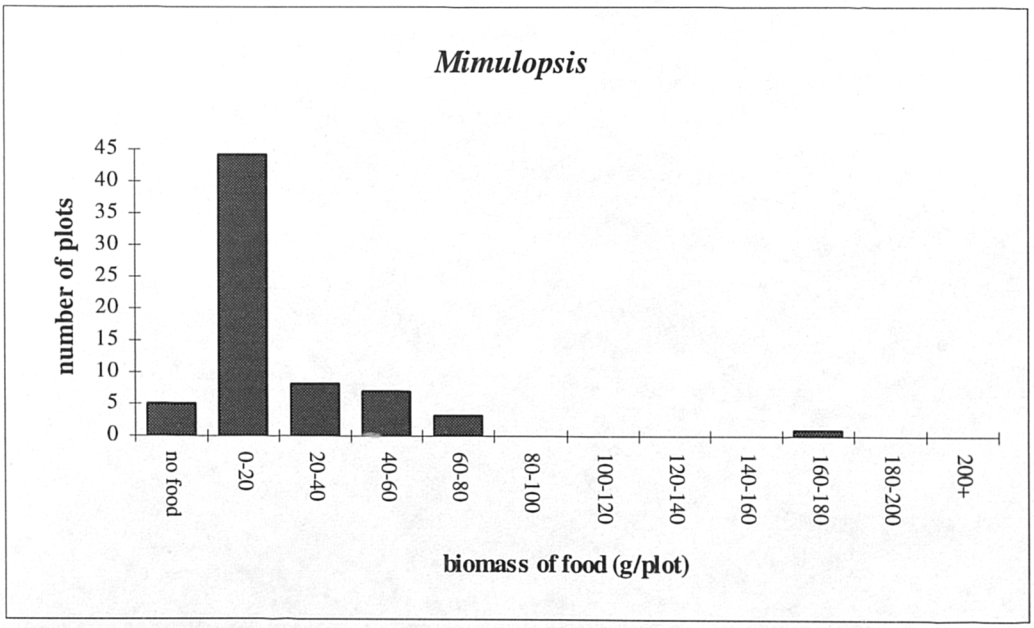

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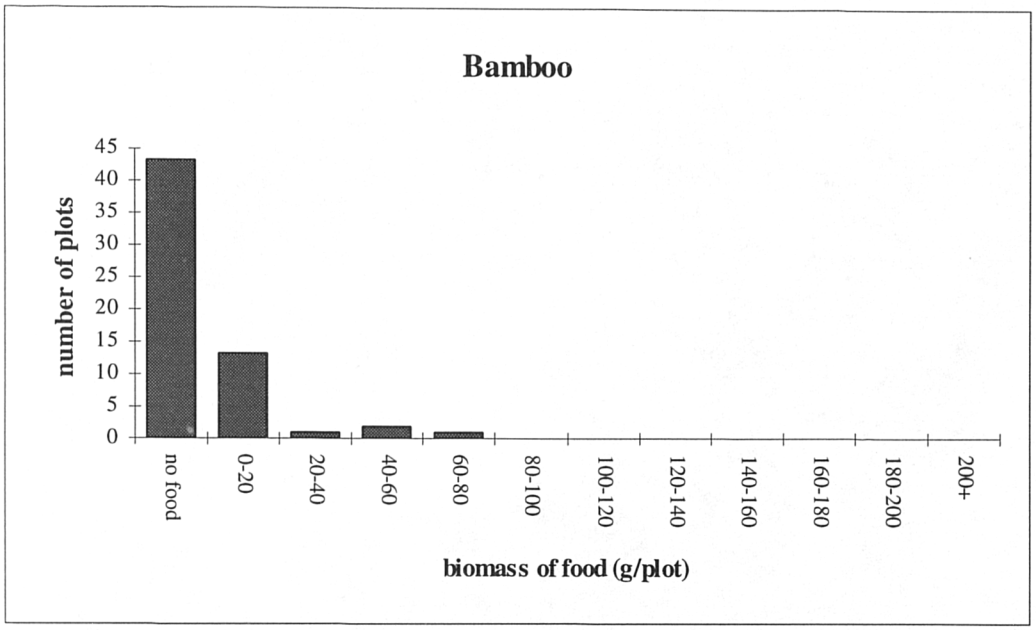


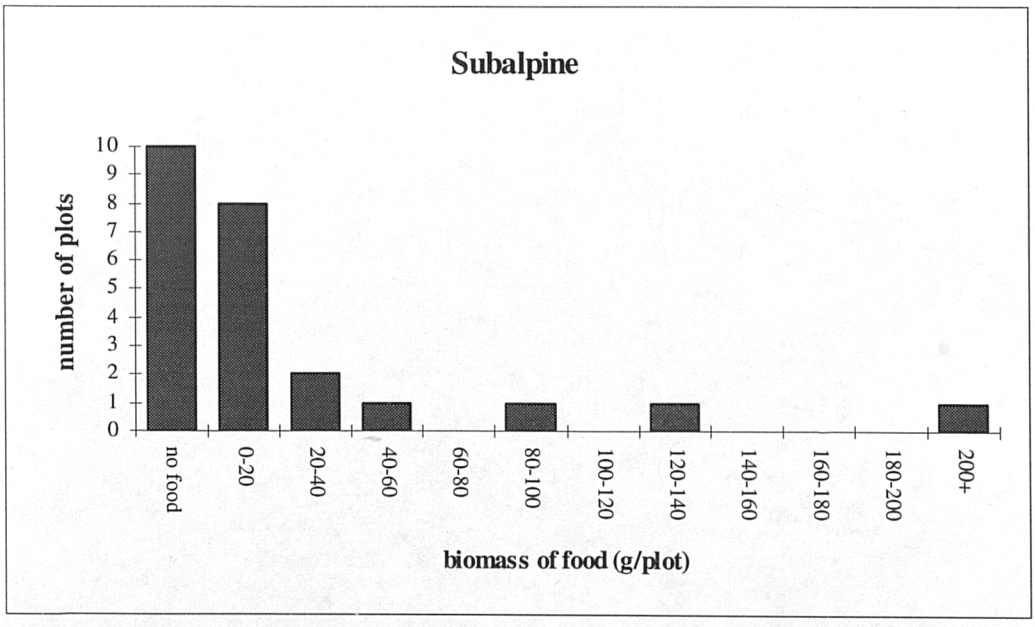


Table 2.4. Nonparametric multiple comparisons of means tests on the biomass of herbaceous foods in each habitat type. The differences are in the direction column > row, and * indicates $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Habitat		HB	HA	MF	MS	BR	SA	BA
HB	Herbaceous	-						
HA	*Hagenia*	**	-					
MF	Mixed forest	***		-				
MS	*Mimulopsis*	***	*		-			
BR	Brush ridge	*				-		
SA	Subalpine	***	**				-	
BA	Bamboo	***	***	***	***			-

Table 2.5. Nonparametric multiple comparisons of means tests on the number of food species per plot in each habitat type. The differences are in the direction column > row, and ** indicates $p < 0.01$ and *** $p < 0.001$.

Habitat		HB	MF	MS	HA	BR	SA	BA
HB	Herbaceous	-						
MF	Mixed forest		-					
MS	*Mimulopsis*			-				
HA	*Hagenia*	**	**		-			
BR	Brush ridge					-		
SA	Subalpine	***	***	***	**		-	
BA	Bamboo	***	***	***	***			-

significant (Kruskal-Wallis, $H = 146$, $d.f. = 6$, $p < 0.001$). Nonparametric multiple comparisons indicated that the differences were significant between both Herbaceous and Mixed Forest and four of the five other habitats (Table 2.5). Significantly fewer herbaceous food species per plot were found in Subalpine and Bamboo than any of the other habitats except Brush Ridge. The lack of significant differences found between Brush Ridge and any other habitat might again have been due to the low sample size in that habitat. The overall pattern was similar to the biomass of herbaceous foods, with the exception of *Hagenia*, which appeared to have fewer species per plot relative to food biomass, compared with other habitats.

The total number of herbaceous food species in each habitat (i.e. species richness) varied considerably between habitats from just 6 in Subalpine to 23 in Mixed Forest. The Shannon-Weiner index was used to compare diversity of foods, which also varied between habitats (Table 2.3). Species richness was found to be inversely correlated with the mean altitude of plots measured in each habitat (Spearman rank correlation, $r_S = -0.81$, $p < 0.05$). Bamboo is an unusual habitat in that the majority of it consists of almost monospecific stands of one species. When this habitat was excluded, diversity showed a very close inverse correlation with altitude ($r_S = -0.94$, $p < 0.05$) and the correlation between richness and altitude was improved ($r_S = -0.90$, $p < 0.05$). Neither biomass of foods, nor percentage of plots containing food were significantly correlated with altitude, but mean number of species per plot showed an inverse correlation with altitude ($r_S = -0.94$, $p < 0.05$) when Bamboo was excluded from the analysis.

2.4 DISCUSSION

Both this and previous studies (Watts, 1983; Plumptre, 1991) have found heterogeneity within habitats in the composition of the vegetation and the biomass of

gorilla foods at individual sampling points. This could be used to argue against making generalisations about habitat quality and gorilla ecology based on these habitats. However, as in previous studies, considerable differences were also found between habitats in both the individual food species and the overall biomass, diversity and richness of foods. This, along with the clear differences in vegetation structure visible on the ground, provides reasonable justification for their use.

Of the seven habitats sampled, Herbaceous and *Hagenia* contained the highest biomass of food, although all of the others contained appreciable quantities, with the exception of Bamboo. The number of species at single sampling points was higher in Herbaceous, while species richness and diversity were higher in *Hagenia.* While these two habitats contained the highest biomass, *Mimulopsis* and Mixed Forest also contained a wide range of foods, both at the level of individual sampling points and at the habitat level. Richness and diversity were both higher in these two habitats than any other. Although bamboo shoots have been reported as seasonally important food items in the diet of certain gorilla groups (Watts, 1984), the biomass of food within this habitat was low even during that season. In general food was ubiquitous; the percentage of sampling plots at which food was present was high in all habitats except Subalpine and Bamboo. However, the amount of food in each plot varied considerably, indicating a patchy distribution of food, as found in previous studies (Watts, 1983).

It is difficult to define precisely how the quality of gorilla habitat should be measured, especially without detailed nutritional analysis of the foods present, which was beyond the scope of this study. However the results indicate that Subalpine, Brush Ridge, Herbaceous, *Hagenia*, *Mimulopsis* and Mixed Forest could all be utilised as gorilla habitat, as they provide food resources. Bamboo maybe seasonally important, but provides considerably less food than these other habitats. Although Subalpine contains significant quantities of food, it is particularly patchily distributed.

Experience indicated that most of the herbaceous food is concentrated in the lower part of the altitudinal range covered by this habitat.

No relationship was found between biomass and altitude, in contrast to Plumptre (1991) who found an inverse correlation. However this study measured the biomass of gorilla foods only, and it is likely that these form a smaller proportion of the total biomass of herbaceous vegetation at lower altitudes. Waterman *et al.* (1983) found that the vegetation in the higher altitude habitats around Karisoke contained low levels of plant secondary compounds compared to other lower altitude forests. The lower habitats in the Virungas might be expected to resemble more closely such other sites, so that a lower proportion of the vegetation would be available to the gorillas as food. In this study both richness and diversity were found to be inversely correlated with altitude, while Plumptre (1991) found this pattern with richness but the opposite with diversity. This could also be due to the difference in measurements made and the wider altitudinal range of habitats sampled in this study.

This study found that a larger proportion of the Virungas consists of potential gorilla habitat than indicated by Weber & Vedder (1983). The large area of Mixed Forest on the northern side of the range contains appreciable quantities of gorilla foods and several groups of gorillas were found in this area in recent censuses (Sholley, 1991; Aveling & Aveling, 1989). There are also patches of *Mimulopsis* habitat throughout other areas indicated by Weber & Vedder (1983) as being inhabitable only seasonally by gorillas, which do provide gorilla food all year round.

The habitat map illustrates well how the study site around the Karisoke Research Centre differs from the rest of the Virungas. Mixed forest and *Mimulopsis* are absent from that region, and only a very small area of Bamboo, which covers much of the remainder of the range, is present. The Karisoke area contains large proportions of

both *Hagenia* and Herbaceous habitats, which contain the highest biomass of food, and is thus one of the richer parts of the forest in terms of food availability.

The main aim of this chapter was to obtain an improved understanding of the availability and quality of habitat over the whole range of the Virungas. As such it was necessary to extrapolate to some extent from areas actually surveyed and sampled to areas of the same appearance on aerial photographs. In particular the area of Mixed Forest habitat actually sampled was relatively small because of the limited time that was available to work in Zaire, so that extrapolations to a much larger area should be treated with caution. However, the overall map of the habitat types produced provides a valuable basis for investigating the habitat utilisation patterns of the gorillas and thus assessing the carrying capacity of the whole ecosystem. It has been shown that there is considerable variation between habitat types both in the gorilla food species available and in the overall biomass, richness and diversity of foods. Such variation is predicted to have implications for the size, ranging behaviour, habitat utilisation and dietary patterns of gorilla groups in the Virungas. The utilisation by the gorillas of these habitats and the food resources which they contain form the subject of the next two chapters.

CHAPTER THREE

MOUNTAIN GORILLA RANGING BEHAVIOUR AND HABITAT UTILISATION

3.1 INTRODUCTION

An animal's habitat provides the food and cover essential for its survival; an understanding of the patterns of habitat utilisation of a species is therefore of great importance in wildlife management. Patterns of mountain gorilla ranging and habitat utilisation have been studied by various authors in the section of the Virungas around the Karisoke Research Centre in Rwanda. Fossey (1974) found that the presence of other gorillas appeared to be the strongest determinant of ranging patterns of one study group over a five year period, although it was suggested that food distribution may play some role in movements between habitats or parts of the range. Avoidance of poaching threat has also been suggested as an important factor underlying ranging behaviour (Fossey, 1974; Elliott, 1976). Fossey & Harcourt (1977) argued that ranging patterns were related to a combination of social factors and, to a lesser extent, food distribution. Caro (1976) also suggested that food supply regulated the movements of solitary males, although Yamagiwa (1986) found that the movements of other groups, rather than the distribution and abundance of food, influenced movements of another solitary male.

Watts (1983, 1987, 1991) and Vedder (1984) were the first investigators to make detailed measurements of the availability of food and other indices of habitat quality in different areas and habitats within the ranges of gorilla groups in the Karisoke study site. Both found that gorillas' strategies of movement and habitat used increased foraging efficiency and that the distribution and abundance of food was the

primary influence on ranging patterns. Watts (1991) suggested that interactions with gorillas and poaching risk have proximate effects superimposed on this.

Gorillas in other areas of the Virungas might face quite different ecological situations from those in the Karisoke study site. The habitat types in other areas are quite different, particularly at lower altitudes (Chapter 2). However little is known about the ecology of mountain gorillas outside the Karisoke study site. In addition, studies within this site have tended, through necessity, to concentrate on one or two groups. The main aim of this chapter was to investigate the ranging patterns of mountain gorillas across a wider cross-section of the Virungas, with the intention of gaining an improved understanding of the range of habitats suitable for gorillas and of which habitat types are relatively most important for the population. This chapter also aimed to investigate relationships between habitat quality, group size and range size. In addition to their theoretical ecological interest, these relationships could be used to predict the ranging behaviour of other groups, both real and hypothetical, and allow crude estimates to be made of the carrying capacity of the Virungas in terms of the number and size of groups that the available habitat could support.

Habitat selection can be seen as occurring at two levels (Aebischer *et al.*, 1993). Firstly a group or individual chooses a home range from within a larger area of potential habitat, often arbitrarily defined, and secondly may use habitat types selectively within that range. This study used two different approaches to investigate habitat selection at these two levels. Firstly crude data on the home ranges of six groups across the Virungas collected by the trackers and guides who monitor research and tourism groups were used to gain an overview of home ranges. These data did not provide detailed information on the habitat utilisation within ranges, which was investigated by examining in more detail the trail signs of two main study groups in contrasting habitats.

Specific hypotheses to be tested were:

1. Group size is positively correlated with food density. Intragroup feeding competition is thought to limit group size (Wrangham *et al.*, 1993), and will be related to the density of food in a given area.
2. Range size is positively correlated with group size. Larger groups are predicted to need larger areas to meet their nutritional requirements.
3. Range size is inversely correlated with food density. Ranges are predicted to be larger in poorer areas, as groups will need a larger area to meet their nutritional requirements.
4. Group size is positively correlated with the total biomass of food within the home range. Despite the predicted relationship between food density and group size, if food resources determine ranging patterns, group size is predicted to be correlated with total food in range, which takes account of variation in both food density and home range size.
5. Day journey length and distance between feeding sites are longer in areas of low food density. Animals foraging efficiently should minimise the distance travelled in order to obtain sufficient resources (S.A. Altmann, 1974). Animals in poorer environments are therefore predicted to have to travel further.
6. Gorillas are selective in the habitats they use within their ranges, preferring those with a high abundance and frequency of food. Previous studies of gorilla ranging have found such selectivity in habitat utilisation within the Karisoke study site (Plumptre, 1991; Watts, 1991).

3.2 METHODS

3.2.1 Ranging patterns of monitored groups

In order to obtain an overview of the patterns of ranging of gorilla groups within the Virungas, a system was established whereby the trackers and guides who monitor groups daily for research or tourism drew sketch maps of the location of each group each day. Karisoke Research Centre staff have made such daily reports for several years and that system needed little modification. Guides visiting tourist groups on both the Rwandan and Zairean side of the forest were trained to make similar reports. It was found that with knowledge of the area the location of each group could be established on a 250 m grid using known footpaths, hills and other landmarks which were marked on the sketch maps. The assumption used in the analysis was that fixes were rarely more than one grid square out.

A total of ten groups were monitored in this way. Of these one split up and another was repeatedly lost during the study. Another two were monitored from a guide station in Zaire where the reporting system was not maintained. Data were collected for six groups, each for a complete year between December 1991 and August 1993, including the two main study groups mentioned below. These groups are referred to by the names used locally, Beetsme's group and Group 5 are Karisoke study groups, Group 11 and Susa group are Rwandan tourist groups, and Ndungutsi's group and Rafiki's group are Zairean tourist groups. Gaps existed in the data from some of these groups where monitoring was stopped when the civil war threatened that particular area or when particular guides who were unfamiliar with the system visited those groups. The minimum number of daily fixes was 187 and this number was used for all groups in the analysis of home ranges. The mean consecutive number of days of the gaps in the data from the group with the minimum number of fixes was seven. Blocks of days of this length were removed

at random from the datasets of the other groups, to give a comparable pattern of fixes for all groups.

The location of each group each day was plotted on a 1:100,000 contour map of the Virunga area to which footpaths and other key features had been added, along with a 250 m grid. Minimum convex polygons (MCP; Mohr, 1947; Southwood, 1966) were constructed around these locations using a home range analysis program, "Atrack", developed by D. Rogers at the University of Bristol. Gorilla groups make occasional forays outside their normal ranges, producing outlying fixes. Such fixes can have a disproportionate effect on the size of an MCP (Harris *et al.*, 1990), so any single fix which added more than 10% to the area was removed. The digitised habitat map of the Virungas described in Chapter 2 was imported into the IDRISI GIS software package and the outlines of the MCP home ranges and core areas digitised into this system. For the MCP outlines the coordinates of the mid-point of each grid square were used. The ranges and core areas of each group were then superimposed on the habitat map and the areas of each habitat type within each calculated using IDRISI. No attempt was made to correct the calculates areas for slope, for the reasons outlined in Chapter 2.

In order to obtain an outline of the areas within each range most frequently occupied by each group, core areas were defined using an adaptation of the method described by Samuel *et al.* (1985). This method is based on grid cells and outlines those areas which are used more intensively than would be expected if the entire home range was used randomly. Each cell in the grid was included in the core area if the number of fixes in it and the surrounding eight cells was greater than the number that would be expected in nine cells if fixes were distributed evenly across the MCP home range. This method thus took account of the error in locating fixes using the sketch maps drawn by the trackers, which meant that in some cases fixes might have been in a neighbouring cell.

Estimates of the total biomass of food and the average food density in each MCP home range and core area were calculated using the density of food in each habitat from the vegetation surveys described in Chapter 2, weighted by the area of each habitat type in the range. The size and composition of each group was obtained from the records of the Volcano Veterinary Centre and from a recent census (Sholley, 1991). Estimates of the biomass of each group were made using published estimates of 200 kg for an adult male and 100 kg for an adult female (Goodall, 1977) and estimates of 75 kg and 50 kg for sub-adults and juveniles respectively. Group biomass was used in preference to number of individuals in the analyses as a more meaningful measure. Pearson correlations were used to investigate the relationships between these variables. One-tailed tests were used as directional hypotheses had been made.

3.2.2 Habitat utilisation by the two main study groups

More detailed data were collected on the ranging behaviour and habitat use of the two main study groups, Beetsme's group in the Karisoke study area and Group 11 in the Visoke-Sabinyo saddle. Mountain gorillas generally leave clear trails as they move through the forest and feed at distinct sites which are visible along the trail. In the course of collecting the data on diet presented in Chapter 4, 112 complete day of trail between consecutive night nest sites of these two groups were followed between March 1991 and February 1992. A total of 9986 feeding spots along 73 km of trail were examined, divided between the two groups (n = 5337 for Beetsme's group and n = 4649 for Group 11). Trail length was measured by pacing, pace size being checked frequently against measured 50 m distances in comparable terrain. A continual note was made of the location of the trail using altitude, compass bearings and proximity to known landmarks. The habitat type

through which the trail passed was also noted. This allowed the total journey length, the mean distance between feeding sites and the proportion of feeding sites in each habitat type to be calculated for each day's trail.

MCP home ranges were constructed using the mid-point of each day's trail, which with more accurate positional data than provided by the sketch maps described above, could be located on a 100 m grid. Outlying fixes were not removed because with the smaller number of fixes it was not certain whether an area with just one fix was really outside the normal home range. The ranges were digitised into IDRISI and the areas of each habitat type within each measured as described above. The total biomass of food and food density in each MCP home range was also estimated as before.

Patterns of habitat use were analysed using the compositional method described by Aebischer *et al.* (1993), comparing the proportion of feeding sites in each habitat as a measure of utilisation with the area of each in the MCP home ranges over the same period as a measure of availability. This method circumvents the problem of non-independence of consecutive fixes. Clearly the location and habitat type of adjacent feeding sites would not be independent. However, the proportion of feeding sites in a particular habitat along a trail does provide a good estimate of the proportion of that group's feeding time in that habitat on that day. Aebischer *et al.* (1993) used the proportion utilisation of each animal as the basis for the analysis of patterns of habitat use within the population. In this study each day's trail was used as the sampling unit in the analysis of the habitat utilisation of each group.

3.3 RESULTS

3.3.1 Ranging patterns of monitored groups

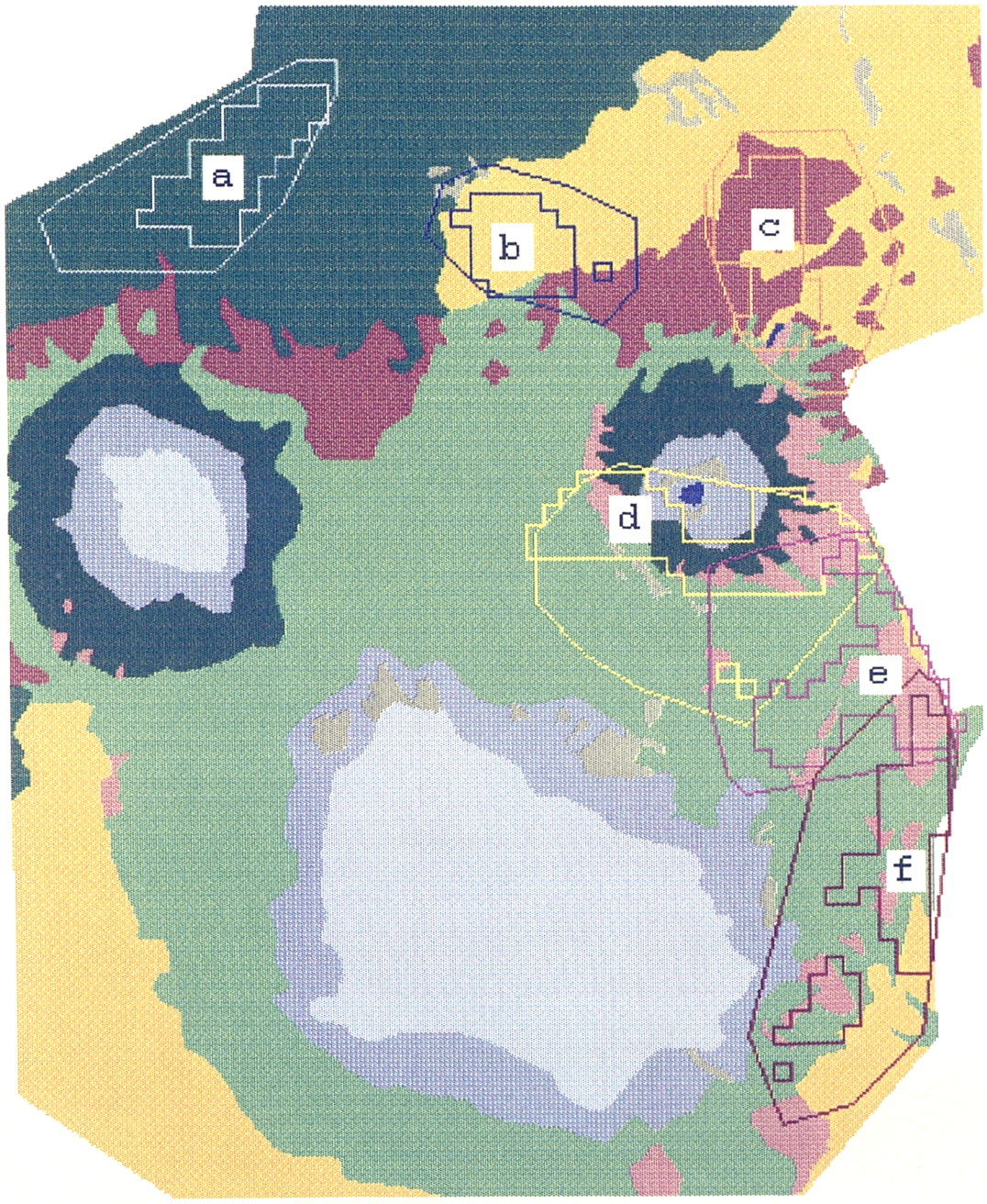
Considerable variation was found in the habitat types which made up the home ranges and core areas of the six monitored groups across the Virungas. Figure 3.1 shows these superimposed on the habitat map described in Chapter 2, and the area of each habitat in each home range is given in Table 3.1. The ranges of these six groups between them included all the habitat types in the Virungas with the exception of Alpine. There was little overlap in habitats used between the three groups in the lower saddle area north of Mount Visoke (Group 11, Rafiki's group and Ndungutsi's group) and the other three in the higher altitude region around Mounts Karisimbi and Visoke. The home range of Ndungutsi group consisted almost entirely of Mixed Forest, while those of Group 11 and Rafiki's group included a mixture of Bamboo and *Mimulopsis*. Group 5, Beetsme's group and Susa group's home ranges comprised largely of *Hagenia* and Herbaceous with variable areas of Bamboo, Brush Ridge and Subalpine habitats.

The six groups varied in size between 10 and 28 individuals (excluding dependent infants) which corresponded to a range of group biomass between 1025 and 2775 kg. There was also variation in the sizes of the home ranges (4.7 to 12.4 km^2) and core areas (2.1 to 5.2 km). The estimated total biomass of food within ranges varied by a over a factor of ten and the density of food also varied considerably between ranges. Data on these parameters are given in Table 3.2.

There are three reasons for considering Beetsme's group to be anomalous. Firstly their home range was either shifting or enlarging and during the course of the study of the group used a considerable area of forest for the first time (*personal observation*). Secondly the group only formed in 1986 and was continuing to grow

Figure 3.1. The MCP home ranges (outer lines) and core areas (inner lines) of each of the six study groups, superimposed on the central section of the habitat map of the Virungas shown in Figure 2.2. Core areas were defined as described in the text. The six groups are a) Ndungutsi's group, b) Rafiki's group, c) Group 11, d) Beetsme's group, e) Group 5 and f) Susa group. The scale is 1:100 000 (1 cm equals 1 km).

Ranges of monitored groups



Alpine
Subalpine
Brush Ridge
Herbaceous
Hagenia
Bamboo
Mimulopsis
Mixed Forest
Meadow
Water

Table 3.1. The areas in km^2 of each habitat type in the MCP home ranges of the six groups monitored by trackers and guides. Habitats are arranged approximately in order of descending altitude

Habitat	**Beetsme**	**Group 5**	**Susa**	**Group 11**	**Rafiki**	**Ndungutsi**
Subalpine	1.17	0.07	0.41			
Brush Ridge	1.64	0.21				
Herbaceous	1.79	2.57	2.00	0.17		
Hagenia	7.42	7.02	7.17	0.55	0.20	
Bamboo		0.14	2.20	2.69	3.42	
Mimulopsis				4.20	0.75	0.04
Mixed Forest					0.19	6.90
Meadow	0.31	0.01			0.10	
Lake	0.09			0.03		
Total size	12.42	10.01	11.78	7.64	4.66	6.94

Table 3.2. Group size, group biomass, and the area and habitat quality parameters of the MCP home ranges and core areas of the six groups monitored by trackers and guides.

	Beetsme	Group 5	Susa	Group 11	Rafiki	Ndungutsi
Group size	13	28	25	10	10	16
Group biomass (kg)	1350	2775	2250	1425	1025	1525
Area of:						
MCP range (km^2)	12.4	10.0	11.8	7.6	4.7	6.9
Core area (km^2)	5.2	3.8	4.2	3.0	2.1	2.9
Food biomass:						
in MCP (*1000 kg)	770.7	732.7	719.5	150.1	48.5	144.8
in core area (*1000 kg)	279.6	280.2	286.4	62.3	20.2	61.1
***Food density*:**						
in MCP (*1000 kg/km^2)	61.0	73.2	61.0	19.6	10.4	20.9
in core area (*1000 kg/km^2)	54.3	73.5	68.7	21.1	9.5	20.9

in size. Thirdly they shared the majority of their home range with another group of five young adult males. Although some degree of overlap of ranges is not uncommon (Fossey & Harcourt, 1977; Figure 3.1), none of the other groups in this study shared such a large portion of their range with a single, other group. These factors could be expected to complicate the relationships between group size, range size and food density. For this reason Beetsme's group is excluded from certain of the analyses described below and is shown as an open square in Figures 3.2 to 3.5.

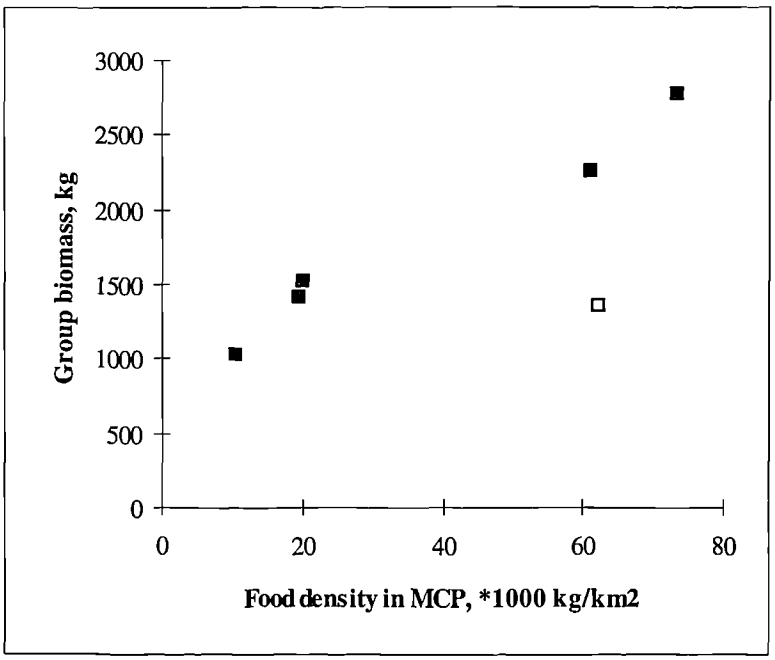
The relationships between group biomass and food density are shown in Figure 3.2. Positive correlations were found between group biomass and density of food in both home ranges and core areas. When Beetsme's group was excluded, both relationships were close to linear correlations. Correlation coefficients and significance levels are given in Figure 3.2.

Home range size and group biomass were less closely related (Figure 3.3). If all groups were included, there was only a weak (non-significant) correlation with both home range size and core area size. However, when Beetsme's group was excluded, significant positive correlations were found between group biomass and both home range size and core area size.

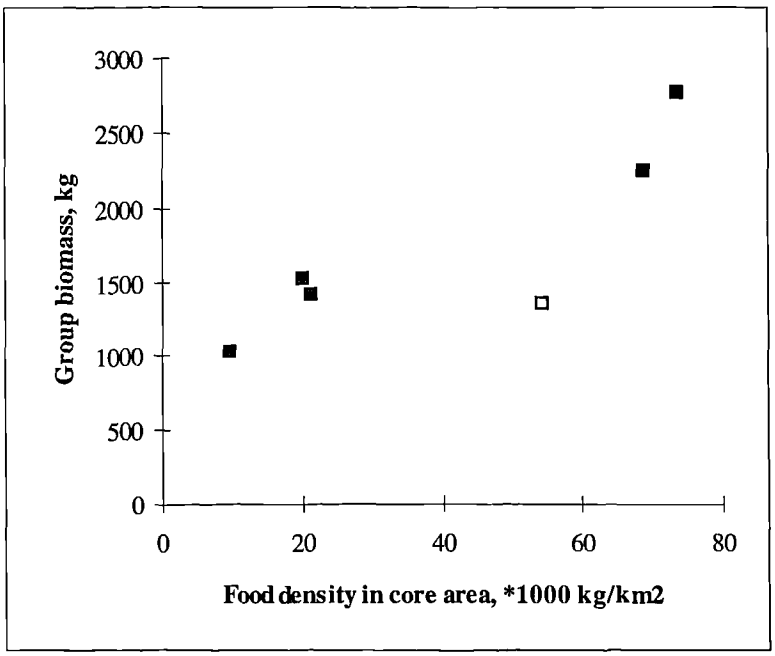
The predicted inverse correlation between food density and range size or core area size was not found (Figure 3.4). The situation was in fact reversed, a positive correlation was found between these variables. The inclusion or otherwise of Beetsme's group made little difference to these relationships.

Finally, positive correlations were found between group biomass and the total estimated biomass of food in the home range and in the core area (Figure 3.5). These were significant when Beetsme's group was excluded from the analysis.

Figure 3.2. The relationship between group biomass and food density in the MCP home range and the core area of each of the six monitored groups. Beetsme's group is shown as an open square, for reasons described in the text. The correlation coefficients (r) and one-tailed significance levels are given for each correlation, including and excluding Beetsme's group.

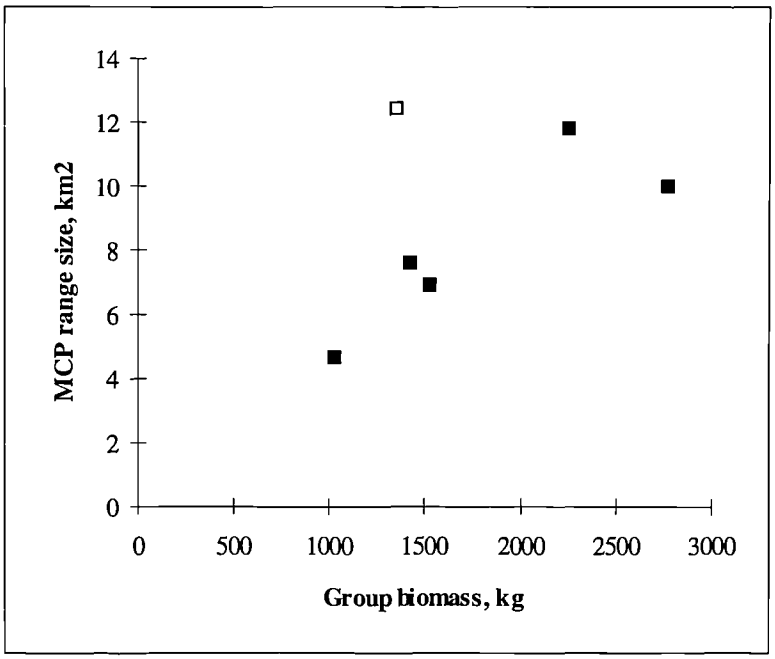


with Beetsme's group: $r = 0.77$, $p = 0.037$
without Beetsme's group: $r = 0.98$, $p = 0.001$

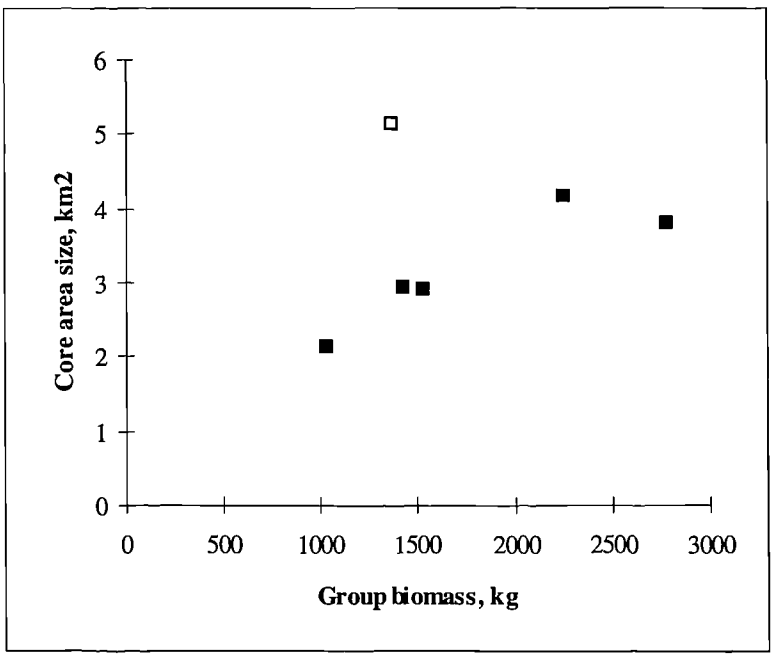


with Beetsme's group: $r_s = 0.84$, $p = 0.018$
without Beetsme's group: $r = 0.97$, $p = 0.003$

Figure 3.3. The relationships between group biomass and the size of the MCP home range and the core area of each of the six monitored groups. Beetsme's group is shown as an open square, for reasons described in the text. The correlation coefficients (r) and one-tailed significance levels are given for each correlation, including and excluding Beetsme's group.

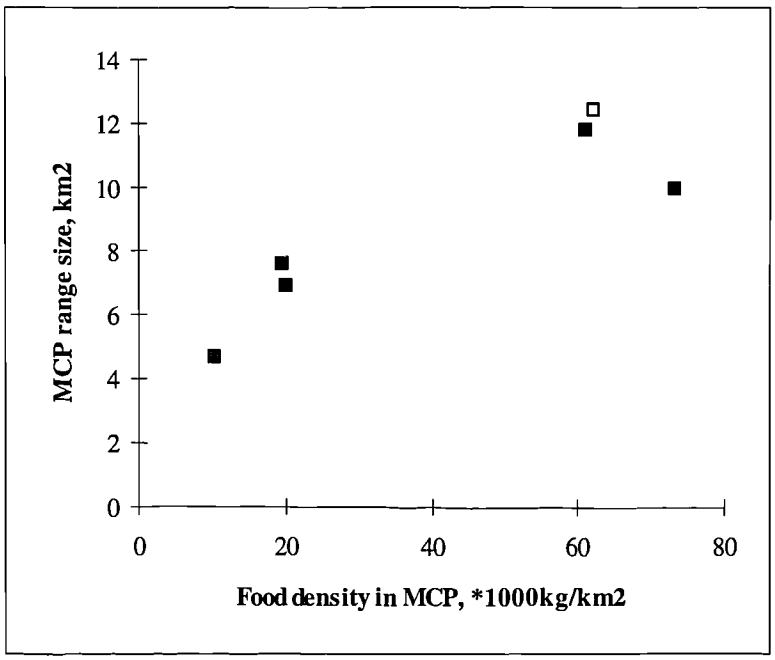


with Beetsme's group: $r = 0.52$, $p = 0.14$
without Beetsme's group: $r = 0.86$, $p = 0.03$

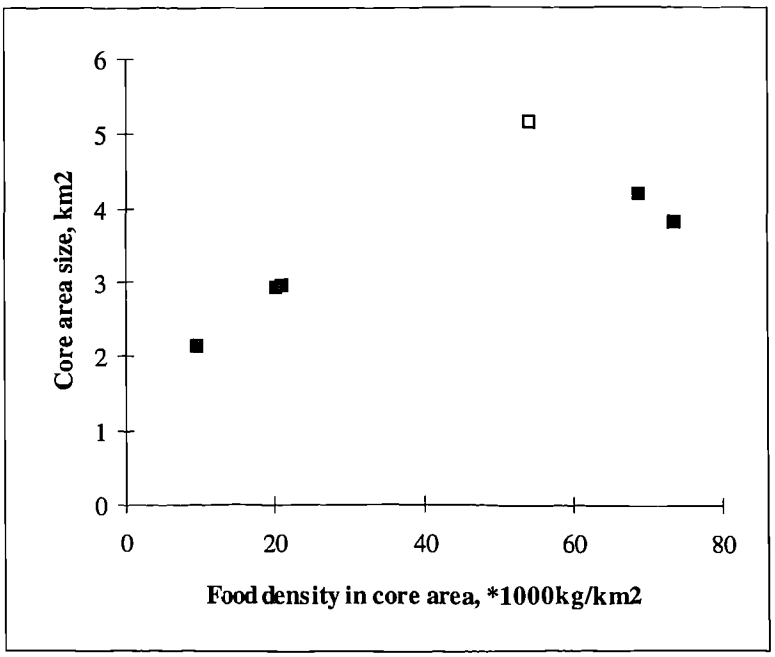


with Beetsme's group: $r = 0.37$, $p = 0.24$
without Beetsme's group: $r = 0.90$, $p = 0.019$

Figure 3.4. The relationship between MCP home range and core area size and food density for each of the six monitored groups. Beetsme's group is shown as an open square, for reasons described in the text. The correlation coefficients (r) are given for each correlation including and excluding Beetsme's group. The correlations are in the opposite direction from the original one-tailed hypotheses, so that it is inappropriate to quote one-tailed significance levels. The two-tailed significance levels are given in parentheses, so as to indicate the significance of these unexpected correlations.

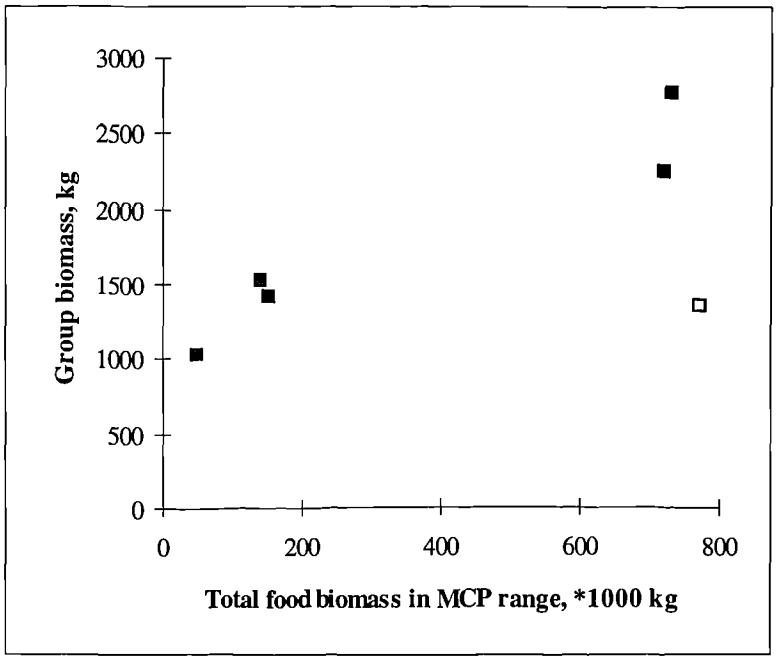


with Beetsme's group, $r = 0.89$, ($p = 0.017$)
without Beetsme's group, $r = 0.89$, ($p = 0.044$)

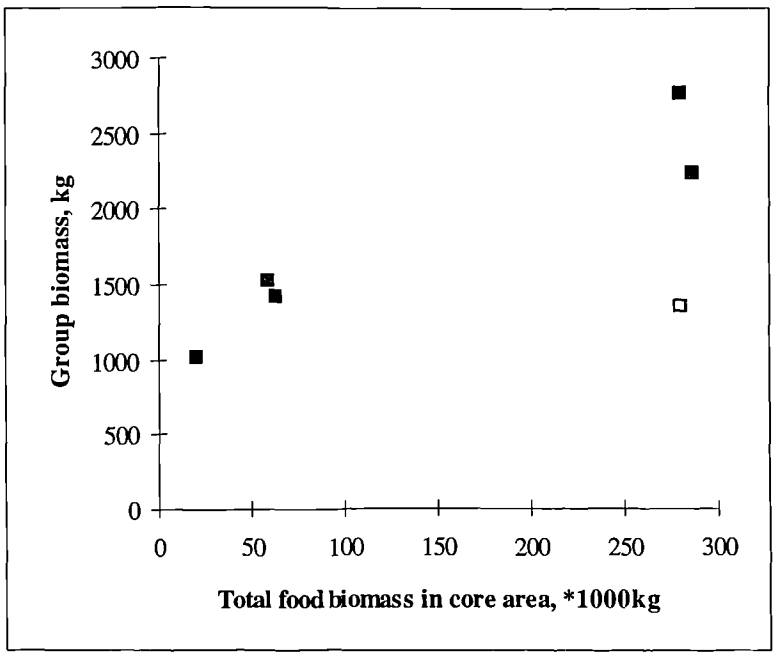


with Beetsme's group: $r = 0.78$, ($p = 0.065$)
without Beetsme's group: $r = 0.94$, ($p = 0.017$)

Figure 3.5. The relationship between group biomass and the estimated total food biomass in the MCP home range and core area for each of the six monitored groups. Beetsme's group is shown as an open square, for reasons described in the text. The correlation coefficients (r) and one-tailed significance levels are given for each correlation, including and excluding Beetsme's group.



with Beetsme's group: $r = 0.66$, $p = 0.075$
without Beetsme's group: $r = 0.95$, $p = 0.006$

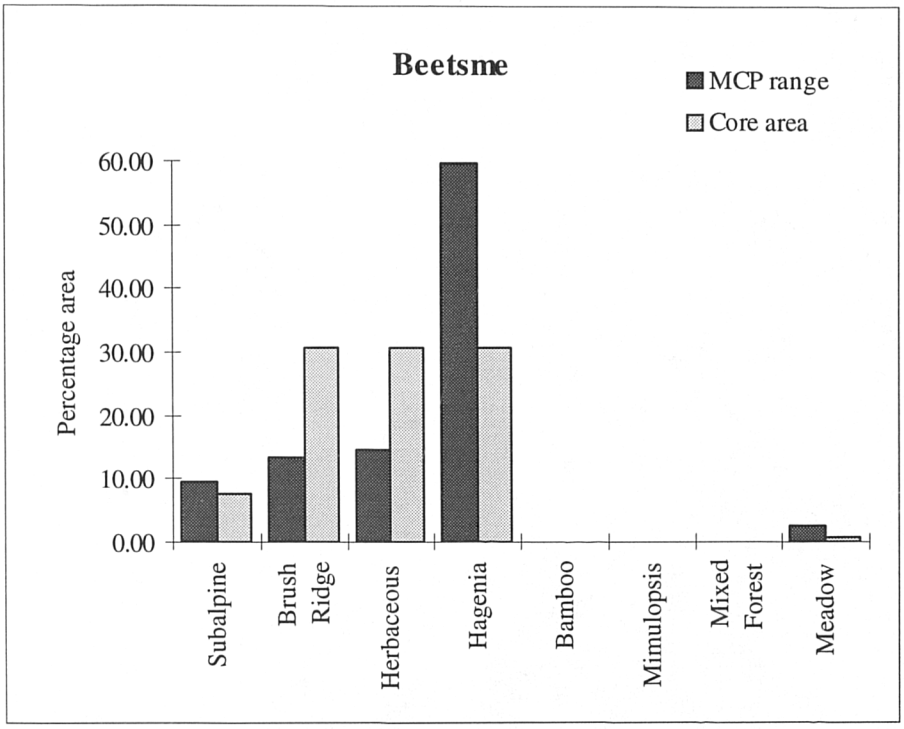


with Beetsme's group: $r = 0.70$, $p = 0.062$
without Beetsme's group: $r = 0.95$, $p = 0.007$

In most of the graphs in Figures 3.2 to 3.5, the six groups cluster into two groups of three. This is particularly evident in the relationship between home range size and food density and between the total estimated biomass of food in the home range and group biomass (Figures 3.4 and 3.5). These clusters correspond to three larger groups with larger ranges in habitats with high food density, and three smaller groups with smaller ranges in poorer habitat. The former were found in the higher altitude region around Mount Karisimbi and the latter in the lower saddle region between Mounts Visoke and Sabinyo. The difference between these two types of home range could itself go some way towards explaining the correlations found.

The relationships found between range size, group biomass and food density described above were the same for both the total home ranges and the core areas. Core areas defined in this way were between 36 % and 45 % of the total home range size. The estimated food density within the core areas of these groups was not significantly different from that in the whole home range (Wilcoxin matched pairs test, $T = 6$, $n = 6$). However, Figure 3.1 suggests that in certain cases, the core areas coincided with patches of particular habitats (particularly in the cases of Group 11, Beetsme's group and Group 5, i.e. ranges c, d and e in Figure 3.3). The percentages of each habitat in each home range and core area are shown in Figure 3.6. Ndungutsi's group is not shown as the home range in this case was virtually all one habitat type, Mixed Forest. The core area of Beetsme's group contained a high proportion of Herbaceous and Brush Ridge relative to the total home range, indicating a positive selection of these two habitats. Both Group 5 and Susa group also selected Herbaceous in this way. Group 11's core area contained a higher proportion of *Mimulopsis* than the overall home range and a lower proportion of Bamboo. The core area of Rafiki's group contained a slightly higher proportion of Bamboo than the home range. Most of the range was made up of Bamboo with smaller areas of other habitats around the periphery.

Figure 3.6. The percentage composition of habitat types in the MCP home ranges and core areas of the monitored groups. Ndungutsi's group is not shown as the range of this group was made up almost entirely of one habitat type, Mixed Forest.



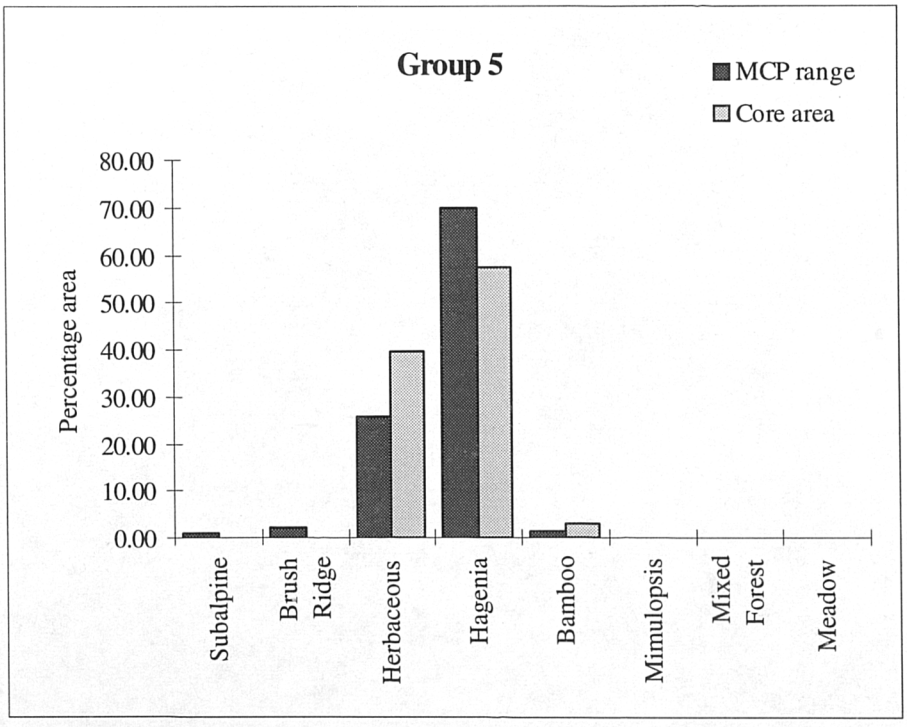
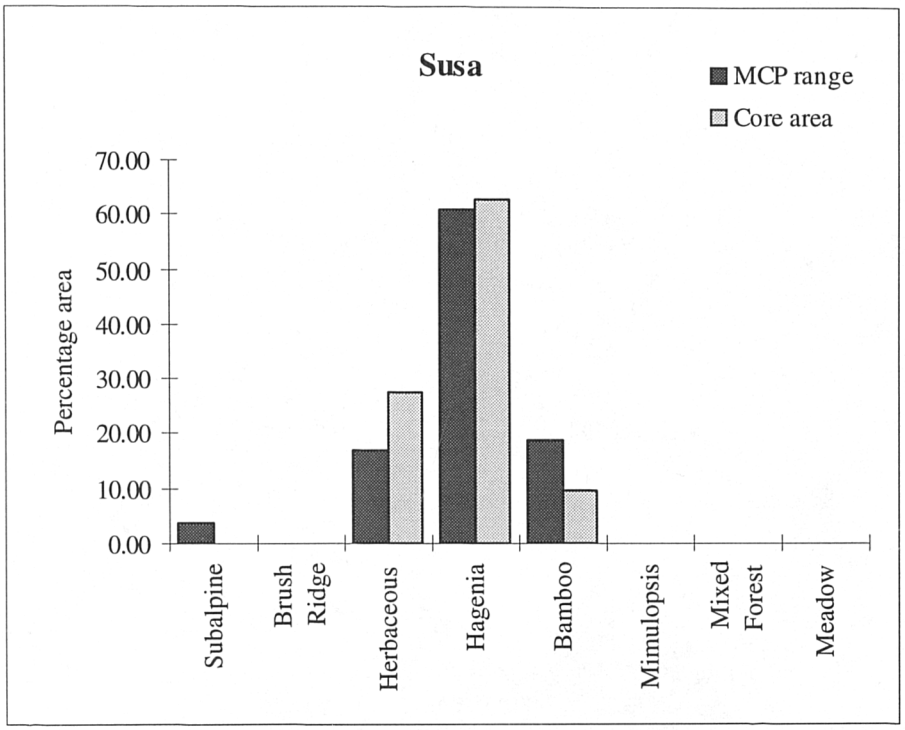


Figure 3.6, continued.



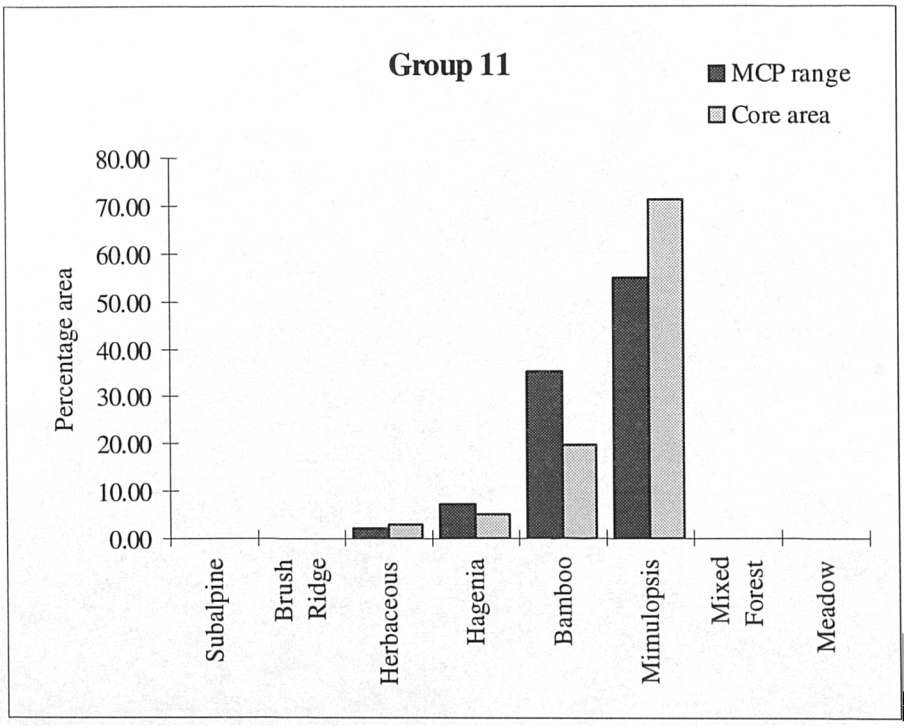
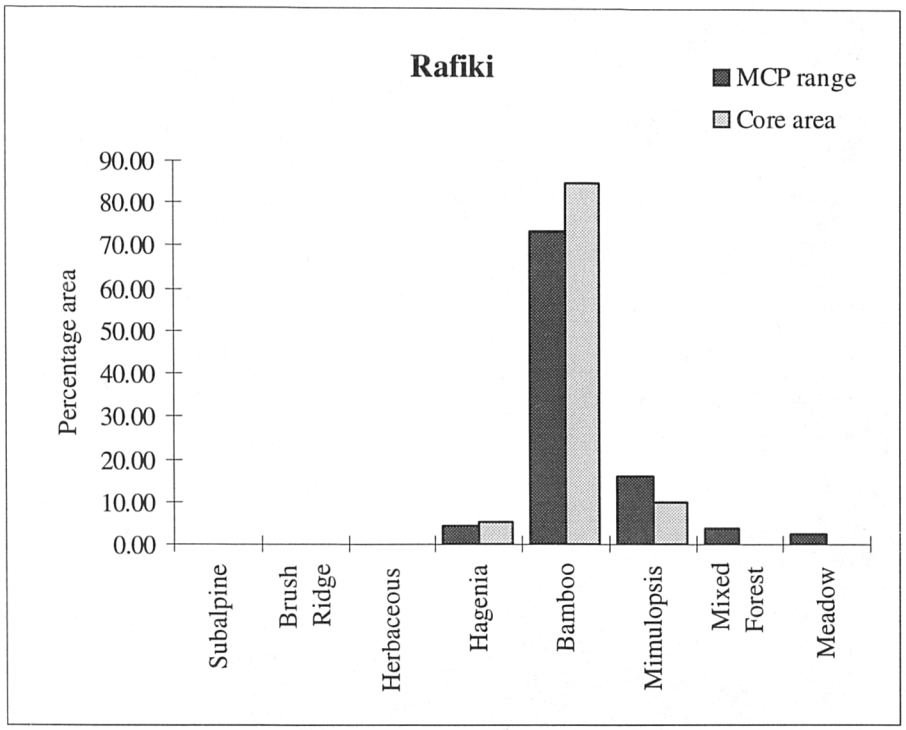


Figure 3.6, continued.



3.3.2 Home range and movement patterns of the two main study groups

The size and composition of the ranges of the two main study groups based on the locations of the mid-points of trails differed from the ranges of the same groups described above, being based on a different dataset over a different one year period. Group 11's home range was smaller when estimated using the trail signs. This could be due to the smaller number of fixes used, but the group did use a smaller area of Bamboo in the east of their home range during that time period. The areas of each habitat type in the home ranges of these two groups based on these data are given in Table 3.3. The percentage overlap in the habitat types used by the two groups was low (5.2 %, calculated as described in Struhsaker, 1975).

These two groups have similar group biomasses (1350 kg for Beetsme's group and 1425 kg for Group 11), yet the home range of Beetsme's group was found to be 2.5 times larger than that of Group 11 (Table 3.4). Both the estimated total biomass of food within the range and the density of food were greater for Beetsme's group. As mentioned above, there are reasons for considering Beetsme's group to be anomalous, in that the group biomass is lower than expected. These groups each represent one of the two contrasting home range types suggested above.

The difference in food density between the two ranges is reflected in the movement patterns of the groups. Group 11, in the area of lower food density, moved further each day ($t = 3.47$, $p < 0.001$) and further between feeding sites ($t = 4.33$, $p < 0.001$) than Beetsme's group (Table 3.4).

Table 3.3. The areas in km^2 of each habitat type in the MCP home ranges of the two main study groups, based on the locations of the mid-points of trails followed. These ranges were measured over a different one year period from those based on tracker's reports shown in Figure 3.1 and Table 3.1.

Habitat	**Beetsme's group**	**Group 11**
Subalpine	0.96	
Brush Ridge	1.44	
Herbaceous	1.11	0.07
Hagenia	7.75	0.17
Bamboo		1.21
Mimulopsis		3.19
Meadow	0.26	
Lake	0.06	0.02
Total area	11.58	4.66

Table 3.4. Comparison of group size, home range parameters and movement parameters of the two main study groups.

	Beetsme's group	**Group 11**
Group size (excluding dependent infants)	13	10
Group biomass (kg)	1350	1425
Range size (km^2)	11.58	4.66
Food biomass in range (*1000 kg)	733.1	87.46
Food density (*1000 kg/km^2)	63.29	18.75
Mean day journey length[1] m ± se	550.5 ± 37.7	756.5 ± 45.8
Mean distance between feeding sites[1] m ± se	6.15 ± 0.39	8.82 ± 0.48

[1] $n = 59$ and $n = 52$ days of trail for Beetsme's group and Group 11 respectively.

3.3.3 Utilisation of habitat by the two main study groups

Feeding sites of the two main study groups were found within four habitat types in each range. Ivlev's electivity index indicates that Beetsme's group selected Herbaceous and Brush Ridge habitat, using these two more than would be expected if habitat utilisation was random so that habitats were used in proportion to their availability (Table 3.5). Group 11 showed a positive selection of *Mimulopsis* in the same way. These results confirm the pattern of habitat selection indicated by the composition of the core areas relative to the overall home ranges described above.

Compositional analysis (Aebischer *et al.*, 1993) was used to test whether these deviations were significantly different from random utilisation. Log-odds-ratios, or "logratios" were calculated from the proportion of feeding sites in each habitat type for each day's trail and from the proportion of each habitat within the home range, using one habitat as the denominator. The logratio is calculated as $\ln (x_i / x_j)$ where x_i is the proportion of habitat i used or available and x_j is the proportion of the habitat selected as the denominator. For n habitats, $n - 1$ logratios are thus produced. The difference between the logratios for use and availability were calculated for each day. If habitats are used at random, the average over all days of each logratio difference should equal zero. Multivariate ANOVA of the logratio differences provides a simultaneous test over all habitat types of this hypothesis. Wilk's lambda (λ) is a suitable statistic for the test. Both Beetsme's group and Group 11 were found to use habitats in a significantly non-random way ($\lambda = 0.541$, $d.f. = 3, p < 0.001$ and $\lambda = 0.190$, $d.f. = 3, p < 0.001$ respectively).

Compositional analysis can also be used to rank habitat types in order of relative use and to identify where significant non-random use occurs (Aebischer *et al.*, 1993). This is equivalent to comparing all possible pairs of habitats, which can be done using logratios differences. Table 3.6 shows the mean logratio differences for each

Table 3.5. The use, availablity and electivity of habitat types in the MCP home ranges of the two main study groups. Ivlev's electivity index is calculated as $(r_i - n_i)/(r_i + n_i)$ where r_i is proportion of feeding sites in habitat *i* and n_i is the proportion of habitat *i* in the MCP home range. A positive electivity index indicates a positive selection of that habitat.

Group and Habitat	**Mean daily percentage of feeding sites**	**Percentage of total area of home range**	**Ivlev's electivity index**
Beetsme's group:			
Subalpine	7.6	8.5	-0.055
Brush Ridge	16.7	12.7	0.136
Herbaceous	47.8	9.8	0.659
Hagenia	27.6	68.8	-0.427
Group 11:			
Herbaceous	1.3	1.5	-0.071
Hagenia	3.7	3.7	0
Mimulopsis	80.7	68.8	0.080
Bamboo	14.1	26	-0.297

pair of habitats, replaced by signs for ease of interpretation. Rows correspond to the habitat type in the numerator of the logratio, columns to the denominator; a positive sign indicates selection of the row habitat relative to the column habitat and a negative sign *vice versa*. Where a mean logratio difference is significantly different from zero (one sample *t*-test), this represents a significant difference in the relative use of the two habitats. The number of positive elements in each row can be used to rank the habitat types, a complete row of positives indicating that a habitat is used more than expected relative to all other habitats. Moreover, the individual tests indicate where significant differences in ranking occur. The habitat rankings for the two main study groups are shown in Table 3.7.

Aebischer *et al.* (1993) suggest using a protected least significant difference procedure to determine significance levels, but others do not recommend this procedure (Zar, 1984). All but one of the probability levels of the *t*-tests in Table 3.6 are very small ($p < 0.001$) and the ANOVA procedure did indicate significant differences from random in the overall pattern of habitat utilisation. Such procedures were therefore not considered necessary.

The relationships between habitat rank and various parameters of habitat quality are shown in Table 3.8. No single habitat parameter obviously accounted for the rank position of the habitats used by either group. The habitat which ranked highest for Beetsme's group, Herbaceous, had a high density and frequency of food and a high mean number of food species per 1 m^2 plot, as described in Chapter 2. Brush Ridge ranked higher and *Hagenia* ranked lower than expected on the basis of these parameters. Brush Ridge generally forms a mosaic pattern between patches of Herbaceous (Figure 2.2), so that the group would inevitably have utilised Brush Ridge as it moved between patches of Herbaceous. A large part of the *Hagenia* habitat across the centre of the home range of Beetsme's group had a particularly grassy understorey (*personal observation*) and thus would have provided less gorilla

Table 3.6. Simplified habitat ranking matrices for the two main study groups. The mean logratio difference for each pair of habitats was calculated and replaced by its sign. Positive signs thus indicate a positive selection of the row habitat relative to the column habitat and a negative signs vice versa. A triple sign indicates a significant difference ($p < 0.05$) in the relative use of the two habitats; a single sign indicates a non-significant difference. Ranks are from 0 (lowest) to 3 (highest). See text for further explanation.

Beetsme's group:

Habitat	Subalpine	Brush Ridge	Herbaceous	*Hagenia*	**Rank**
Subalpine	.	- - -	- - -	-	0
Brush Ridge	+++	.	- - -	+++	2
Herbaceous	+++	+++	.	+++	3
Hagenia	+	- - -	- - -	.	1

Group 11:

Habitat	Herbaceous	*Hagenia*	*Mimulopsis*	Bamboo	**Rank**
Herbaceous	.	+	- - -	-	1
Hagenia	-	.	- - -	-	0
Mimulopsis	+++	+++	.	+++	3
Bamboo	+	+	- - -	.	2

Table 3.7. Habitat selection rankings for the two main study groups. Ranks are given separately for Group 11 during the bamboo shooting season (mid-October to mid-January) and the rest of the year, in addition to the overall rankings. Habitat A > Habitat B indicates that Habitat A was positively selected relative to Habitat B. A significant difference ($p < 0.05$) between two consecutively ranked habitats is denoted by > > >. See text for additional explanation.

Group	**Rank order of habitat selection**
Beetsme's group:	
overall	Herbaceous > > > Brush Ridge > > > *Hagenia* > Subalpine
Group 11:	
overall	*Mimulopsis* > > > Bamboo > Herbaceous > *Hagenia*
bamboo season	*Mimulopsis* > Bamboo > > > Herbaceous > *Hagenia*
rest of year	*Mimulopsis* > > > Herbaceous > *Hagenia* > Bamboo

Table 3.8. Habitat preference rankings (1 is lowest, 4 highest) and habitat quality parameters for the habitat types within the home ranges of the two main study groups. The estimation of habitat quality parameters is described in Chapter 2. Certain parameters are given separately for Bamboo during the season when shoots are present.

Habitat type	Rank	Food density g/m2	Frequency of food[1]	Plot richness[2]	Habitat richness[3]	Habitat diversity[4]
Beetsme's group :						
Herbaceous	4	74.94	100	2.44	13	1.85
Brush Ridge	3	17.36	80	1.60	8	1.83
Hagenia	2	75.99	92	1.70	20	2.03
Subalpine	1	37.68	58	0.70	6	1.67
Group 11:						
Mimulopsis	4	20.08	93	2.01	20	2.32
Bamboo	3	4.21	28	0.38	11	1.19
(with shoots		6.32			12	1.43)
Herbaceous	2	74.94	100	2.44	13	1.85
Hagenia	1	75.99	92	1.70	20	2.03

[1] The percentage of 1 m^2 plots containing herbaceous food.
[2] The mean number of herbaceous food species in each 1 m^2 plot.
[3] The number of herbaceous food species found in that habitat.
[4] Shannon-Wiener index.

food than the average for this habitat. The estimates of the quality of that habitat, made from measurements across a wider area of the Virungas, would therefore have overestimated the quality of it within the home range of Beetsme's group. This could explain the unexpectedly low ranking of *Hagenia*.

The most selected habitat for Group 11 was *Mimulopsis*. This habitat did not have as high a density of foods as Herbaceous or *Hagenia*, but did have a high frequency and species richness (Table 3.8). Overall, *Mimulopsis* was selected more than Bamboo, which had particularly low habitat quality parameters. Herbaceous and *Hagenia* ranked lower than expected on the basis of food density, but only a small area of each occurred at one edge of Group 11's range.

For Group 11, the complete year could meaningfully be split into the bamboo shooting season (mid-October to mid-January) versus the rest of the year. Extending the multivariate ANOVA described above to include this distinction as a factor allowed the effect of season on the overall pattern of habitat utilisation to be statistically tested. This effect was found to be significant ($\lambda = 0.614$, $d.f. = 3$, $p < 0.001$). The habitat ranking procedure was repeated separately for trail days during the bamboo season ($n = 11$) and the rest of the year ($n = 42$). These rankings are also shown in Table 3.7. Bamboo habitat ranked higher during the bamboo season (not significantly different from *Mimulopsis*) than during the rest of the year. However, the density of food in Bamboo during that season was not much higher than during the rest of the year, despite the presence of bamboo shoots (Table 3.8).

3.4 DISCUSSION

Positive correlations were found between group biomass and three other variables: food density, home range size and the total biomass of food in the range. However the last two of these relationships were only clear when one group, Beetsme's, was excluded from the analyses. The Virunga gorilla population is increasing and is likely to be below carrying capacity (Sholley, 1991). It is therefore quite possible that some groups are smaller than would be expected on the basis of the habitat which they occupy. The fact that the inclusion or otherwise of Beetsme's group made little difference to the correlation between food density and range size suggests that the home range size of Beetsme's group was not anomalous, at least in relation to habitat quality, but that the group size was. If the biomass of the all male group which shared the majority of the home range of Beetsme's group (approximately 800 kg) was included, the biomass of Beetsme's group would fit these correlations much more closely. However, this all male group dispersed during the course of the study and it is uncertain that their range coincided exactly with that of Beetsme's group, so simply adding their biomass to that of Beetsme's group in the analyses was not justified. Gorilla groups are not constant over long periods of time, undergoing a cycle of growth and fission or dispersal with the death of the dominant male (Yamagiwa, 1987). It could be argued that Beetsme's group was not really anomalous, but merely represented a certain stage in this cycle. However, even on this basis, excluding this group from the analyses would be expected to clarify the relationships between group biomass, food density and home range size. Moreover, the correlations between group biomass and food density and between food density and home range size are clear even when Beetsme's group is included.

It could be argued that parametric correlations (i.e. Pearson) should not be used with such small sample sizes as the number of monitored groups used to investigate

the relationships between group size, food density and home range size shown in Figures 3.2 to 3.5. Normal probability plots for each variable, with the exception of the total food in the home range, did give good approximations of straight lines, consistent with a normal distribution. Spearman rank correlations would not utilise much of the information in Figures 3.2 to 3.5. When Spearman correlations were calculated for these relationships, significance levels were reduced, but the pattern of results was not altered.

3.4.1 Group size and food density

The positive correlation found between group size and food density was as predicted given the assumption that intragroup feeding competition is a constraint on group size (Hypothesis 1). Such competition has been considered important in determining group size in primates in general (Beauchamp & Cabana, 1990; Wrangham *et al.*, 1993) and in the great apes in particular (Wrangham, 1986; Malenky & Stiles, 1991; Malenky & Wrangham, 1994; Malenky *et al.*, 1994). This discussion has focussed on the patch size or ubiquity of different food sources, principally fruit trees and terrestrial herbaceous vegetation (THV), and the role of patch size in determining levels of feeding competition. However Watts (1983) found mountain gorilla food (which is primarily THV) in the Virungas to be distributed in many small patches, and a group would be unlikely all to feed in one patch at one time. However the density of food, determined by both the size and the density of these patches, could still determine the level of intragroup feeding competition if, as seems likely, there is a limit on how widely dispersed individuals could be while still remaining part of a coherent group.

3.4.2 Range size: general pattern and underlying factors

The home ranges of six groups sampled in this study included the majority of the habitat types present in the Virungas. Only Alpine, which occurs above around 3600 m and contains virtually no gorilla food, was not represented in any of the ranges. Three of the ranges (Ndungutsi's group, Rafiki's group and Group 11) are comprised largely of habitat described by Weber and Vedder (1983) as virtually unusable by gorillas, or habitable seasonally or by extremely low numbers. Clearly mountain gorillas are more flexible in their habitat requirements than previously thought.

Schaller (1963) reported home ranges sizes for mountain gorillas in the Virungas as large as 22 km^2, although it is not stated how the estimates were made. Fossey & Harcourt (1977) believed these figures to be overestimates, and themselves reported yearly range sizes of 4-5 and approximately 8 km^2 for groups in the Karisoke study site. Vedder (1984) and Watts (1991) both report range sizes of about 8 km^2 for two groups in the same area. These figures were calculated by summing the area of grid cells entered by the particular group, which would be expected to underestimate range size relative to the minimum convex polygon method used in this study by allowing the outline of the range to include concave sections. The three groups in or close to the Karisoke study site had ranges of 10 to 12.4 km^2, in general agreement with previous studies in the same area. Those elsewhere were smaller, between 4.7 and 7.6 km^2, but still within the range reported by Fossey & Harcourt (1977).

The relationship between group biomass and home range size was as predicted (Hypothesis 2), a larger group would intuitively be expected to need a larger area of suitable habitat to meet its nutritional requirements, all other things being equal. Fossey & Harcourt (1977) reported a similar relationship between monthly range

size and group size in mountain gorillas. The correlation found between food density and group size could have been expected to mask the relationship between range size and group size. Larger groups might be expected to need larger areas, but are found in areas of higher food density, which could negate the need for larger ranges. However, in addition to needing a larger area to meet nutritional requirements, larger groups might cause more trampling damage to the vegetation, and thus tend to use a larger area for foraging.

Interspecific variation in home range size has also been found to be correlated with group size in primates (Clutton-Brock & Harvey, 1977), herbivores (Harestad & Bunnell, 1979) and carnivores (Gittleman & Harvey, 1982; Harestad & Bunnell, 1979). Within species, group size influences home range size in, for example, several species of baboon, *Papio* spp. and *Theropithecus gelada* (Barton *et al.*, 1992; Iwamoto & Dunbar, 1983), wood bison, *Bison bison athabascae* (Larter & Gates, 1994), and coyotes, *Canis latrans* (Bowen, 1982).

Negative correlations between range size and habitat quality or productivity have been found for rhesus macaques, *Macaca mulatta* (Jiang *et al.*, 1991), three species of carnivore (*Felis rufus*, *Canis latrans* and *Ursus americanus*, Gompper & Gittleman, 1991), hispid cotton rats, *Sigmodon hispidus* (Cameron & Spencer, 1985), and meadow voles, *Microtus pennsylvanicus* (Jones, 1990). Several studies comparing a species in areas of high and low habitat quality have found range size to be larger in the latter (e.g. wood bison, Larter & Gates, 1994; woodmice, *Apodemus sylaticus*, Gorman & Ahmad, 1993; red squirrels, *Sciurus vulgaris*, Wauters & Dhondt, 1992; howler monkeys, *Allouatta palliata*, Estrada, 1984; Barbary macaques, *Macaca sylvanus*, Mehlman, 1989). In an analysis of interspecific variation, home range size was found to be inversely correlated with productivity for herbivores, carnivores and omnivores (Harestad & Bunnell, 1979). However other studies have found that it is the distribution of food patches, rather

than the density of food that determines range size (e.g. red foxes, *Vulpes vulpes*, Macdonald, 1981; Blanford's fox, *Vulpes cana*, Geffen *et al.*, 1992; European badgers, *Meles meles*, Kruuk & Parish, 1982). In red deer, *Cervus elaphus*, home ranges size is negatively correlated with the proportion of good grazing or favoured habitats in the range (Clutton-Brock *et al.*, 1982; Catt & Staines, 1987).

In this study the predicted inverse relationship between food density and home range size (Hypothesis 3) was not found. The positive correlation between group size and food density would be expected to confound this relationship. That is, in areas of high food density range sizes would be expected to be small, but group sizes would be large. If group size is positively correlated with range size, this could mask the predicted relationship between food density and home range size. Although range size was not found to be larger in habitat with lower food density within the range of habitats within the Virungas, much larger ranges of 31 km^2 (Casimir & Butenandt, 1973) and 34 km^2 (Goodall, 1977) have been reported for eastern lowland gorillas (*Gorilla gorilla graueri*) in Kahuzi-Biega National Park, Zaire. Goodall (1977) attributes this difference to differences in the abundance and availability of food resources.

The population density and the presence of other groups might also contribute to variation in range size. Home range size is inversely correlated with population density in howler monkeys, *Allouatta* spp. (Crockett & Eisenberg, 1987). However the population density of gorillas in the Karisoke study area, where the largest ranges were found, is higher than the average for the whole of the Virungas (Weber & Vedder, 1983; Plumptre, 1991). Also, the home ranges in this area overlap considerably (Figure 3.1) and given this overlap it is unlikely that increasing population density would result in smaller home ranges. The degree of overlap of the ranges of the other three groups with neighbouring groups is unknown.

The positive correlation found between food density and range size was not predicted. Overall, group biomass, home range size and food density were all positively correlated. That is there was, apparently, a continuum in mountain gorillas in the Virungas between large groups occupying large home ranges in areas of high food density and smaller groups in smaller ranges with lower food densities. In fact the groups in this study fell into two types at either end of this spectrum, and it cannot be concluded that there is continuous variation along it. The pattern found could be explained in the following way. The majority of the gorilla food in the habitats most prevalent in the larger, richer ranges, Herbaceous and *Hagenia*, consist of herbaceous plants. These are not only eaten by the gorillas, but flattened as the gorillas move around. They might therefore be expected to take longer to regenerate after a group has fed on them than the leaves of vines which make up the bulk of the food present in the lower altitude habitats where the smaller, poorer ranges are found. In other words food density might not always be directly correlated with productivity. This could explain how the gorillas in the latter type of habitat might need a smaller area to meet their nutritional requirements, despite the lower food density.

Plumptre (1994) found that trampling by large mammalian herbivores in the Virungas, including gorillas, was unlikely to cause a significant reduction in the available biomass of vegetation. Watts (1983) did find some evidence that regeneration rates affected revisitation rates. However revisitation rates were more closely related to the food availability in the area and some evidence has been found that gorilla foraging actually increases the productivity of the food plants (Watts, 1983, 1987). More detailed studies of the regeneration rates of gorilla foods in different habitats and their role in determining ranging patterns would be required to elucidate these issues.

3.4.3 Movement patterns

Foraging pathways which minimise the distance travelled in order to obtain a given amount of food will be optimal (S.A. Altmann, 1974). Watts (1991) found both day journey length and distance between feeding spots in each habitat type to be inversely correlated with food biomass (= density in this study) as well as certain other parameters of habitat quality for one group of mountain gorillas as would be predicted if animals foraged in this way. Comparing these movement parameters in two groups, this study found both to be longer for the group with the poorer range, in terms of food density, in agreement with Watts' (1991) findings. This difference was as predicted (Hypothesis 5). Group size would also be expected to affect these movement parameters (Iwamoto & Dunbar, 1983; Watts, 1991; Barton *et al.*, 1992; Olupot *et al.*, 1994), however the two groups in this study had a very similar biomass. Yamagiwa & Mwanza (1994) found that solitary male eastern lowland gorillas in Kahuzi-Biega National Park also moved further per day and between feeding sites than solitary mountain gorilla males in the Virungas where food is more densely and evenly distributed. Similar relationships between movement patterns and habitat quality have been found for other species including baboons, *Papio* spp. (Barton *et al.*, 1992; Henzi *et al.*, 1992), hoolock gibbons, *Hylobates hoolock* (Mukherjee, 1986) and chipmunks, *Tomias townsendii* (Rosenberg & Anthony, 1993).

3.4.4 Habitat utilisation

The two main study groups were both found to use habitat types selectively as predicted (Hypothesis 6). Certain types were used more than would be expected if habitat utilisation was random so that habitats were used in proportion to their availability. Some of this selectivity was related to differences in food availability

between habitats, indicating that the groups increased their foraging efficiency by spending more time in higher quality habitats. However certain other factors may be important, most notably the configuration of habitat types within the home range of each group. Thus Brush Ridge may have been selected by Beetsme's group because it tends to occur between patches of another preferred habitat, Herbaceous. Also, group 11 might have failed to show positive selection of Herbaceous or *Hagenia* despite the high food densities in these habitats because they occurred only in small patches on one side of their home range. This begs the question as to why the group selects the home range which they do; presumably either factors such as the presence of other groups are important, or the quality of *Mimulopsis* as a habitat might be higher than suggested by the food density measure used. The fact that Bamboo was selected to approximately the same degree as *Mimulopsis* during the bamboo shooting season despite a low food density also indicates that food density is not the only predictor of habitat selection. In this case it may be that the presence of particularly favoured food items (bamboo shoots).

Vedder (1984) found that one group spent more time (measured by frequency and length of visits) in higher quality areas of their home ranges, so increasing foraging efficiency from a random pattern of ranging. Watts (1991) found a similar pattern for another group, including correlations between both the total time spent in each habitat and the habitat use intensity (time/area of habitat in home range) and food availability. Prior to this study, only Plumptre (1991) had tested for departure from random habitat selection in mountain gorilla habitat utilisation. He found that three groups in the Karisoke study area showed selectivity, preferring Herbaceous, and Brush Ridge as in this study. The one group whose home range included Bamboo also showed a preference for it during the wet season, when bamboo shoots were present. This study found a similar pattern of habitat selectivity both within and outside the area where these previous studies were made, although the actual habitats selected were different in other areas.

3.4.5 Conclusions

In conclusion, mountain gorilla groups were found to utilise a wider range of habitats within the Virungas than previously documented. Group biomass was found to be correlated with food density as predicted. Home range size was ? correlated with group size, but was not inversely correlated with food density. Group home ranges tended to fall into two main types. These relationships, along with the pattern of availability of habitats obtained in Chapter 2, will be used in Chapter 6 to estimate the carrying capacity of the Virungas for gorillas.

The two main study groups used habitats selectively, in ways that could at least partly be related to food availability (as predicted by Hypothesis 6). The two open herbaceous habitats, Herbaceous and *Mimulopsis* were positively selected by gorillas, along with Brush Ridge. Bamboo was selected during the season when bamboo shoots were present, despite the low density of food, suggesting the shoots to be highly preferred food items. The diet of the two main study groups, that is resource selection at the level of individual food items rather than habitats, will form the subject of the next chapter.

CHAPTER FOUR

THE COMPOSITION AND VARIABILITY OF MOUNTAIN GORILLA DIET ACROSS THE VIRUNGAS

4.1 INTRODUCTION

Primate diets have been classified into categories such as insectivore, frugivore and folivore, and related to factors including body size and behavioural and morphological adaptations (e.g. Clutton-Brock & Harvey, 1977; Richard, 1985). However, recent studies have found that many primates exhibit considerable intraspecific variation in diet, often switching between these broad categories (Chapman & Chapman, 1990). Gorillas would be predicted to be folivorous on the basis of their large body size, and several studies of mountain gorillas in the Karisoke Research Centre study site within the Virungas have found this to be the case (Fossey & Harcourt, 1977; Watts, 1984; Plumptre, 1991, 1995). Mountain gorillas rely heavily on perennially available foliage of herbs and vines and show considerable specialisation on plant parts and species, a pattern facilitated by the richness of the habitat (Watts, 1984).

Recent studies of western lowland gorillas, however, have found their diet to consist of a much larger number of foods than mountain gorillas, including significant quantities of fruit (Tutin & Fernandez, 1985; Rogers *et al.*, 1990; Williamson *et al.*, 1990; Nishihara, 1992). Eastern lowland gorillas in Kahuzi-Biega National Park in Zaire have also been found to consume a greater number of foods and large quantities of fruit, when available (Goodall, 1977). Goodall (1977) characterises the environment in Kahuzi-Biega as more variable and containing less abundant year-round food supplies than the Virungas. Jamagiwa & Mwanza (1994) found a

similar pattern when comparing the diets of solitary adult males in lowland forest in Kahuzi-Biega with those in the Virungas.

As described in Chapters 2 and 3, mountain gorillas occupy a wider range of habitats than those represented in the Karisoke study site. This site is at the uppermost end of the altitudinal range occupied by gorillas in the Virungas, and different habitats types, notably Bamboo, *Mimulopsis* and Mixed Forest, are utilised in other areas. The altitude of the lower habitats is comparable with that of Goodall (1977)'s study site in Kahuzi-Biega. These habitats contain a different array of potential foods from those found in the Karisoke study site, with a lower total biomass of available food.

Foraging theory predicts that an animal will respond to reduced availability of food by expanding its diet to include lesser quality foods, travelling further in order to find enough of the same foods, or a combination of the two (Schoener, 1971; Vedder, 1984). The former would be predicted if search costs are high and the value of alternative foods is not significantly lower than those already eaten, while the latter is expected if search costs are low or alternative foods are of little value. Mountain gorillas have been found to travel further in lower quality habitats (Watts, 1991; Chapter 3) and times of low rainfall, where rainfall is assumed to be correlated with food availability (Vedder, 1984).

The aim of this chapter was to investigate the variation in gorilla diet across a wider range of habitats within the Virungas than previously studied and thus to investigate the responses of the gorillas to variation in the patterns of availability of food resources. This will provide an improved understanding of how typical the diet of gorillas in the Karisoke study site is of the rest of the population and whether diets elsewhere in the Virungas resemble those of other populations more closely.

The diets of two main study groups, Beetsme's group in the Karisoke study site and Group 11 in the lower altitude saddle region between Mounts Visoke and Sabinyo, are investigated in this chapter. There was little overlap in the habitat types within the home ranges of these two groups, described in Chapter 3. The home range of Group 11 was both smaller than that of Beetsme's group and contained a lower density of food, although the biomass of the two groups was approximately equal. The food density in Group 11's home range was typical of much of the area of the Virungas away from the Karisoke study site. It is predicted that, given the different array of foods available and the lower overall biomass of food in the habitats occupied by Group 11, differences will be found in both the food species consumed and the overall dietary patterns of the two groups. Group 11 is predicted to show a greater dietary breadth and diversity than Beetsme's group.

Where tame or habituated animals are available or visibility is good, direct observation of study animals is generally the most accurate way to investigate diet. Observations have been used successfully in the past in studies of mountain gorilla diet (Watts, 1984; Vedder, 1989). However in this study access to habituated groups was only available in the Karisoke study area, so that a combination of other techniques were needed to investigate diet in other areas. Gorillas tend to feed at distinct sites as they move through the forest and leave signs of food items eaten along their trails. By following trails it was therefore possible to estimate the relative frequency with which different foods are eaten. For most food types it was also possible to estimate the length of stem or number of plants eaten, and thus biomass consumed, at each feeding site. Biomass estimates could only be made, however, for a few leaf foods. Microhistological examination of faecal samples has often been used in studies of herbivore diet (Norbury & Sanson, 1992) and is most effective for leaves. A combination of trail signs and faecal analysis could therefore provide estimates of the biomass eaten of almost all foods, providing comparable estimates could be calculated from the two different methods.

Many studies have shown that faecal analysis as a technique for measuring diet can be inaccurate if different plant species are digested and fragmented to different degrees (Holechek *et al.*, 1982; Norbury, 1988). Norbury (1988) found that correcting for the unidentifiable proportion of each plant species in the faeces greatly improved the accuracy of the analysis. Plumptre (1991) also found that this correction improved estimates of the proportions of hand compounded mixtures of leaves digested *in vitro*. Corrections for the proportion of identifiable cuticle were used in this study. Trail signs have been used in studies of western lowland gorilla diet (Williamson *et al.*, 1990), but little information is available on the accuracy of this method.

In this study a combination of trail signs and faecal analysis was used to investigate the diet of the main study groups. In addition direct observations were made on one habituated Karisoke research group and those data used to evaluate the accuracy of the trail signs and faecal analysis, as well as to check the comparability of these methods. This study thus provides valuable tests of microhistological faecal analysis and trail signs as techniques for measuring diet.

4.2 METHODS

4.2.1 Trail signs

Data were collected on the diet of the two main study groups, Beetsme's group in the Karisoke study area and Group 11 in the Visoke-Sabinyo saddle. A total of 112 complete days trail between consecutive night nest sites of these two groups were followed from March 1991 until February 1992. A total of 9986 feeding spots along 73 km of trail were examined, divided approximately equally between the two

groups (n = 5337 for Beetsme's group and n = 4649 for Group 11). At each feeding spot the food species and plant part eaten were noted, allowing estimates to be made of the relative frequency with which all foods were eaten. Where the gorillas had peeled stems or split branches to consume the pith, the length eaten was estimated. Length estimates were checked periodically with a tape measure. Where roots had been eaten the number of plants uprooted was noted. The number of thistle leaves eaten (*Carduus* spp.) was estimated from the stripped plants left behind. The number and size of bamboo shoots were estimated from the peelings at feeding spots.

Measured lengths of stem of each food species were processed using techniques comparable to those of the gorillas, dried and weighed to give measures of mass per unit length. These were used to convert estimates of length of stems eaten at each feeding spot to biomass. Estimates of the average mass of roots eaten per plant were made during the observations of feeding described below and used to estimate biomass eaten from the number of plants uprooted at each spot. Estimates of mass eaten from bamboo (*Arundinaria alpina*) shoots of 14 size classes were also made during observations. These biomass estimates allowed the overall relative biomass consumed of each food item to be calculated.

4.2.2 Faecal analysis

While following trails samples of faeces were collected, generally from night nest sites. Samples were less than 24 hours old and preserved in 10 % formalin the same day. Dung bolus size can be related to age sex class (Schaller, 1963) and samples were collected separately for juveniles/sub-adults, adult females and mature silverback males. Faeces of older sub-adult blackback males could not be distinguished from adult females. Faecal samples found in one habitat could

contain food plants eaten elsewhere. Samples for each group, season and age class were therefore pooled irrespective of the habitat type in which they were found. Four seasons were defined, two wet (March to May and September to November) and two dry (June to August and December to January).

Samples were washed through two stacking sieves of mesh 1 and 0.05 mm. This separated identifiable fragments of cuticle and other smaller particles which were collected between the two sieves from undigested fibre, seeds and other large fragments. Washing also removed fine particles which adhered to the cuticle and clouded slides. Some studies have used acids or bleach to clear cuticle of adhering epidermal tissue, but this can bias the analysis by reducing the size of fragments (Norbury, 1988). The washing process described above was found to be sufficient. The mesh of the finer sieve was smaller than the minimum size of identifiable fragments of cuticle and no such fragments were found in the residue. Seeds were counted and identified, and the presence of fragments of driver ants (*Dorylus* sp.) was noted.

The fractions of samples containing identifiable fragments were pooled by age class and season and mixed thoroughly. Small quantities mixed with glycerol were spread on two microscope slides and four transects made across each, measuring the area of cuticle fragments with a squared graticule at x 100 magnification. The relative area of cuticle of each species on each slide was calculated and a mean taken of the two slides. Fragments were identified using a reference collection of photomicrographs of leaf cuticles prepared by Plumptre (1991); additional plant species were added to this collection using the same methods. The range of species eaten by the gorillas was known from the trail signs described above and it was possible to identify cuticle fragments to species level within this range.

In order to correct for differential identifiability of plant species, dried samples of each were ground through a 1 mm mesh and digested in pepsin (600 mg in 300 ml of 0.1 M HCl) for 24 hours followed by cellulase (1.875 g cellulase of *Trichoderma viride*, activity 0.02 EU/mg in 300 ml of buffer of pH 4.6) for 72 hours. For each species the area of identifiable and unidentifiable cuticle was measured and the proportion of identifiable cuticle used to correct the estimates of relative area of cuticle. This digestion regime does not closely replicate the digestion in a gorilla gut, but has been used successfully to measure plant digestibilities (Choo *et al.*, 1981) and gave a usable measure of the relative proportion of each species identifiable after digestion.

Finally, in order to convert the estimates of relative area of cuticle to relative biomass of each species consumed it was necessary to correct for variation in the thickness of leaves. Ten leaves of each species were collected from a variety of locations, and the area of each was measured with a square grid overlay. The samples were dried and weighed to give a measure of mass per cm^2. Gorillas ate leaves and stems of *Galium* spp. together, although only leaf cuticle could be identified in the faeces. Samples of *Galium* spp. were separated into leaves and stem, dried and weighed to give an estimate of the proportion of total mass made up by leaf which was then used to correct the relative biomass found in the faeces. A mean of the proportions of foods found in the faeces of each age class was taken, weighted by the contribution of each age class to the diet of the group as a whole. This weighting was calculated from the figures given by Watts (1984) for the consumption of food be each age class per day and the composition of the group.

4.2.3 Observations

Observations of feeding behaviour were made on the two silverback males, five adult females and two juveniles in Beetsme's group in the Karisoke study area. Focal animal sampling (J. Altmann, 1974) was used. Individuals were observed for 30 minutes in a preset random order with all individuals observed once before any were repeated. If after five minutes a focal individual had not fed, that focal period was abandoned and repeated after the next. A total of 231 observation periods were sampled during one wet and one dry season from June to November 1991.

Observation techniques were based on those of Watts (1984). The time spent by the focal animal feeding on each food type was measured to the nearest 5 seconds. Estimates of the quantity of each food eaten were made as follows. The number of handfuls of leaves eaten was counted, and samples judged to be handful size for each age class were collected, dried and weighed. The lengths of stems eaten were estimated and converted to biomass as for the trail signs data described above. The volumes eaten of roots, bark, rotten wood and fungi were estimated and converted to biomass by collecting, measuring, drying and weighing samples. Where visibility was restricted the biomass eaten was estimated from the time spent feeding on each food type, which was more easily observed. An average rate of feeding on that food type for each age class was calculated from the remainder of the observations.

The relative biomass of each food type eaten by the group was calculated from pooled observations of focal individuals within each habitat type. The overall diet was calculated by weighting the diet in each habitat by the index of habitat use calculated from the proportions of feeding sites found in each habitat described in Chapter 3, which gave the best available estimate of the proportional use of habitats by the two groups.

As a more direct check of the trail signs techniques, sites where focal animals had fed on the main stem foods during feeding observations were examined. This was done before adding up the total lengths observed to have been eaten to avoid biasing the estimates made from trail signs. Estimates of length eaten were made using the methods described above from the peelings and split stems left behind, enabling such estimates to be compared with the actual observed length eaten. *Laportea alatipes* and *Urtica massaica* had comparable growth forms and were eaten in the same way, and so were combined.

4.3 RESULTS

4.3.1 Accuracy of faecal analysis

The results of the faecal analysis from Beetsme's group for the two seasons during which simultaneous observations of feeding behaviour were made are shown in Table 4.1. The relative biomass of leaf foods estimated from faecal analysis was correlated with the relative biomass in the observed diet, even before correcting for differential identifiability of plant species (Spearman rank correlations, $r_S = 0.90$, $p = 0.05$, $n = 5$ in both seasons). The correction made no difference to these correlation coefficients. The mean errors, defined as the mean of the absolute values of the differences between percentage scores from faecal analysis and observations, were smaller after correction (3.54 and 5.20 % for the two seasons before correction, 2.42 and 4.82 % respectively after correction), but these differences were not statistically significant (Wilcoxin matched pairs test, $T = 3$, $n = 5$, and $T = 4$, $n = 5$ respectively).

Table 4.1. Comparison of the diet of Beetsme's group estimated by faecal analysis and direct observations for the two seasons during which simultaneous observations of feeding behaviour were made. The columns give the relative area of leaf cuticle, relative biomass, and relative biomass corrected for the proportion of identifiable fragments, estimated from faecal analysis. The last column gives the relative biomass from direct observations, including only those species identifiable in the faecal samples. All figures are percentages.

Food Species	***Area***	***Biomass***	***Corrected* Biomass**	***Observed* Biomass**
June - August :				
Galium spp.	53.1	59.9	56.9	54.2
Carduus nyassanus	44.2	38.1	38.3	34.9
Laportea alatipes	2.2	1.5	4.1	4.6
Rubus spp.	0.5	0.5	0.7	6.1
Droguetia iners	0.1	0.1	0.1	0.2
September - November :				
Galium spp.	69.6	75	73.3	64.9
Carduus nyassanus	28.4	23.4	24.2	20.5
Laportea alatipes	0.5	0.3	0.9	12.6
Rubus spp.	1.1	1	1.4	1.6
Droguetia iners	0.4	0.2	0.2	0.3

The relative biomasses estimated from faecal analysis in two cases, *L. alatipes* in June to August and *Rubus* spp. in September to November, differed considerably from the observed diet. Possible reasons include inaccuracy of the faecal analysis and correction factors, and chance differences in the diet between the days on which observations were made and those when faecal samples were collected. Such differences would be particularly important for less common foods. As these errors were not consistent between the two seasons and the results of the two techniques were not significantly different, no further correction of the results of the faecal analysis was made based on the observational data.

4.3.2 Accuracy of trail signs

The relative biomass in the diet of those food items for which estimates were possible from trail signs are shown in Table 4.2, again for the two seasons with simultaneous observations of diet. In both seasons the biomass estimates from trail signs were closely correlated with estimates from observations (Spearman rank correlations, $r_S = 0.88$, $p < 0.001$ for June to August and $r_S = 0.84$, $p < 0.001$ for September to November, $n = 19$ in each case). The mean errors, defined as above, were small, 0.88 and 1.04 % for the two seasons respectively.

At the level of individual feeding sites, estimates of lengths of stems eaten from trail signs were an unbiased estimate of observed lengths eaten (Table 4.3). Paired *t*-tests showed no significant differences between estimates from trail signs and observations for *Carduus nyassanus*, *Peucedanum linderi* and *L. alatipes/U. massaica* ($t = 0.63$, $t = 0.92$, $t = 1.34$ respectively, $p > 0.1$ in each case, see Table 4.3 for sample sizes). The estimates of biomass from trail signs were not therefore corrected using the observational data.

Table 4.2. Comparison of the diet of Beetsme's group estimated by trail signs and direct observations for the two seasons during which simultaneous observations of feeding behaviour were made. Columns headed 'Trail' give the relative biomass estimated from trail signs, 'Obs' gives estimates from observations, excluding foods for which biomass estimates were not possible from trail signs. All figures are percentages. Plant parts are: st = stem, lf = leaf, ls = leaf and stem eaten together, lb = leaf base, pi = pith from branches, cu = cuticle from the outside of vines, rt = root, sh = shoot.

FOOD		**RELATIVE BIOMASS**			
		June - Aug		**Sept - Nov**	
Species	**part**	**Trail**	**Obs**	**Trail**	**Obs**
Peucedanum linderi	st	25.0	26.0	48.0	53.6
Carduus nyassanus	lf	42.9	34.8	22.6	23.5
Carduus nyassanus	st	18.7	19.8	16.4	9.19
Carduus nyassanus	rt	8.98	10.4	4.16	4.79
Urtica massaica	st	1.38	3.02	4.27	2.47
Laportea alatipes	st	0.61	1.49	3.25	5.77
Senecio johnstonii	pi	1.05	1.94		
Lobelia stuhlmanii	pi	0.91	0.86		
Carex bequaertii	lb	0.12	0.51	0.26	0.08
Crassocephalum ducis-aprutii	st	0.02	0.03	0.01	
Helichrysum formosissimum	lf	0.10	0.45	0.26	
Cyperus mannii	lb	0.05	0.02	0.32	0.24
Laportea alatipes	rt	0.12	0.63	0.18	0.35
Vernonia adolfi-fredericii	pi	0.13		0.06	
Peucedanum linderi	rt	0.01		0.01	
Rumex ruwenzoriensis	st	0.01			
Lobelia giberroa	rt	0.02		0.04	
Urtica massaica	rt	0.01			
Prenanthes subpeltata	cu		0.09		
Arundinaria alpina	sh				0.04
Carduus leptocanthus	st			0.05	
Carduus leptocanthus	lf			0.02	
Discopodium penninervium	pi			0.14	
Galium spp.	cu			0.01	

Table 4.3. Comparisons of the length of stem eaten at individual feeding sites estimated by direct observation and trail signs for Beetsme's group. The ratio trail/observed indicates the error in the trail sign estimate relative to the observed estimate. A mean ratio close to one therefore indicates that the trail signs is, on average, an unbiased estimate. The mean percentage error indicates the accuracy of the estimates. *n* is the number of feeding sites observed and examined for each food species.

Species	***n***	**Mean ratio of trail/observed**	**Mean percentage error**
Carduus nyassanus	19	0.998	18.0
Peucedanum linderi	20	0.996	13.1
Laportea/Urtica	7	0.940	11.7
Lobelia stuhlmanii	2	0.955	12.5

4.3.3 Combining data from trail signs and faecal analysis

The main problem in using two separate techniques for estimating the proportion of different food items in the diet was how to combine the data from each. This was done by relating biomass estimates from both techniques to the frequency estimates which were made from trail signs for all foods eaten. Thus, for example, if the frequency estimates indicated that 50 % of the diet was made up of those foods for which biomass estimates were made from trail signs, then these relative estimates would be scaled to 50 %. This assumes that the relative frequency measure is not biased towards either those species for which biomass estimates were made from trail signs or those estimated from faecal analysis. This assumption can be tested using the observational data collected on Beetsme's group. The percentages of the total diet measured by the two techniques, as estimated from the relative frequencies, were close to those estimated from the observations (Table 4.4), indicating that the data could be combined in this way.

Another method for combining the two techniques would be to use the foods for which biomass estimates could be made from both trail signs and faecal analysis to calculate relative biomass for all foods on the same scale. Unfortunately, only one food item, *Carduus* spp. leaf, was included by both techniques in this way, so that any error in the estimates for this food would be magnified by basing all other foods on it. However, this was used as a cross-check of the above method for combining data from the two techniques.

Table 4.5 shows how data from the two techniques were combined. The method used for combining the data relative to frequency scores gave results which were closely correlated with the observed diet (Spearman rank correlations, $r_S = 0.92$ for June to August and $r_S = 0.90$ for September to November, $n = 15$ and $p < 0.001$

Table 4.4. The percentage of the total diet included by faecal analysis and trail signs, estimated from the relative frequency data, compared with the same percentages estimated from the observational data.

	Estimated using:	
% diet included by:	frequency	observations
faecal analysis	56.4	59.3
trail signs	56.6	54.0

Table 4.5a. Combining the estimates of relative biomass in the diet of Beetsme's group made from trail signs and faecal analysis for June to August. 'Freq' is the relative frequency with which each food was eaten, a measure available for all foods. 'Mass trail' and 'Mass faeces' are the estimates of relative biomass from trail signs and faecal analysis respectively, scaled to the proportion of the total diet included by each technique, as estimated from the frequency estimate. 'Comb (freq)' is the estimates of the two techniques combined in this way and adjusted to give percentages, while 'Comb (*C.n.*)' is the two estimates combined relative to the one food item included by both, *Carduus nyassanus* leaf. 'Obs' is the relative biomass of food items in the diet estimated from simultaneous observations of feeding behaviour. The plant parts are lf = leaf, ls = leaf and stem eaten together, lb = leaf base, st = stem, pi = pith from branches, rt = root.

Species	Part	Freq	Mass trail	Mass faeces	Comb (freq)	Comb (*C.n.*)	Obs
Galium spp.	ls	22.8		31.2	33.3	37.7	32.8
Carduus nyassanus	st	22.0	11.7		12.5	11.0	12.0
Carduus nyassanus	lf	22.0	26.9	21.0	25.6	25.4	21.1
Peucedanum linderi	st	14.9	15.7		16.7	14.8	15.8
Laportea alatipes	lf	9.2		2.2	2.4	2.7	2.8
Senecio johnstonii	pi	0.5	0.7		0.7	0.6	1.2
Rubus spp.	lf	1.5		0.4	0.4	0.4	3.7
Carduus nyassanus	rt	1.9	5.6		6.0	5.3	6.3
Urtica massaica	st	2.0	0.9		0.9	0.8	1.8
Lobelia stuhlmanii	pi	0.5	0.6		0.6	0.5	0.5
Laportea alatipes	st	0.6	0.4		0.4	0.4	0.9
Carex bequaertii	lb	0.3	0.1		0.1	0.1	0.3
Droguetia iners	lf	0.7					0.1
Crassocephalum ducis-aprutii	st	0.2					
Helichrysum formosissimum	lf	0.1	0.1		0.1	0.1	0.3
Cyperus mannii	lb	0.3					
Laportea alatipes	rt	0.3	0.1		0.1	0.1	0.4
Vernonia adolfi-fredricii	pi	0.1	0.1		0.1	0.1	
Total		100.0	62.8	54.8	100.0	100.0	100.0

Table 4.5b. Combining the estimates of relative biomass in the diet of Beetsme's group made from trail signs and faecal analysis for September to November. See Table 4.5a for further explanation.

Species	Part	Freq	Mass trail	Mass faeces	Comb (freq)	Comb (*C.n.*)	Obs
Galium spp.	ls	32.7		42.6	44.4	40.1	39.0
Carduus nyassanus	st	12.8	8.3		8.6	9.6	4.8
Carduus nyassanus	lf	10.9	11.4	14.1	13.3	13.2	12.3
Peucedanum linderi	st	20.4	24.2		25.3	28.1	28.0
Laportea alatipes	lf	13.9		0.5	0.5	0.5	7.6
Rubus spp.	lf	0.5		0.8	0.8	0.7	1.0
Carduus nyassanus	rt	1.4	2.1		2.2	2.4	2.5
Urtica massaica	st	2.0	2.2		2.2	2.5	1.3
Laportea alatipes	st	2.0	1.6		1.7	1.9	3.0
Carex bequaertii	lb	0.5	0.1		0.1	0.2	
Droguetia iners	lf	0.7		0.1	0.1	0.1	0.2
Crassocephalum ducis-aprutii	st	0.1					
Helichrysum formosissimum	lf	0.1	0.1		0.1	0.1	
Cyperus mannii	lb	0.7	0.2		0.2	0.2	0.1
Laportea alatipes	rt	0.6	0.1		0.1	0.1	0.2
Vernonia adolfi-fredricii	pi	0.1					
Carduus leptocanthus	st	0.1					
Discopodium penninervium	pi	0.1	0.1		0.1	0.1	
Total		100.0	50.5	58.1	100.0	100.0	100.0

in both cases). The mean errors, defined as above, were small, 0.65 % and 1.06 % respectively for the two seasons. This method also gave results which closely matched the second method of combining the data relative to *Carduus* spp. leaf (r_S = 1.00 and r_S = 0.99 for the two seasons respectively, n = 15, $p < 0.001$ for both).

4.3.4 Comparisons between Beetsme's group and Group 11

The relative frequency and biomass of all food items recorded in the diet of Beetsme's group and Group 11 are given in Table 4.6. Beetsme's group ate a total of 65 different plant foods from 35 species, while Group 11 ate 72 from 44 species. For Beetsme's group, nine of these foods contributed more than 1 % to the diet by biomass, while 12 contribute more than 1 % to Group 11's diet. In addition, both groups occasionally split open dead stems of various plants, apparently to obtain cocoons or egg cases. Although it was not possible to estimate the biomass consumed of these food items, it was certainly small.

There were considerable differences in the plants species and parts eaten by the two groups. They shared 36 food items from 22 plant species in common. The overlap in diet between the two groups, calculated as described by Struhsaker (1975), was 41.3 % estimated from relative biomass and 33.2 % from relative frequency. Most of this was due to the large proportion of *Galium* spp. eaten by both; excluding this food the overlap was just 6.3 % by biomass and 8.8 % by frequency. Figure 4.1 shows the contribution of the main foods to the diet of the two groups and illustrates how, apart from *Galium* spp., the diets of the two groups were largely comprised of different food items. There were also differences in the food types eaten (Figure 4.2). Most notably Group 11 ate more leaf and less stem than Beetsme's group. This is a reflection of the fact that more of the foods in the home range of

Table 4.6a. The relative frequency and biomass of all foods recorded in the diet of Beetsme's group. Frequency was calculated from the number of feeding sites at which each food was eaten, biomass was calculated where possible either from faecal analysis or from trail signs, as described in the text. Values are percentages. Plant parts are lf = leaf, ls = leaf and stem eaten together, lb = leaf base, pi = pith from branches, rt = root, fl = flowers, dw = dead wood, tw = twigs, cu = cuticle of vine stems, ba = bark, sh = shoot., fr = fruit and fu = fungus.

Species	Part	Frequency	Biomass
Galium spp.	ls	24.41	34.96
Carduus nyassanus	lf	16.72	19.94
Peucedanum linderi	st	15.8	18.54
Carduus nyassanus	st	16.81	10.72
Senecio johnstonii	pi	2.69	5.07
Carduus nyassanus	rt	1.50	4.31
Laportea alatipes	lf	8.21	1.39
Lobelia stuhlmanii	pi	1.44	1.28
Urtica massaica	st	1.44	1.14
Laportea alatipes	st	0.87	0.64
Rubus spp.	lf	1.61	0.60
Helichrysum formosissimum	lf	0.39	0.41
Carex bequaertii	lb	0.73	0.23
Cyperus mannii	lf	0.58	0.20
Droguetia iners	lf	0.64	0.14
Carduus kikuyorum	lf	0.05	0.12
Cyperus mannii	lb	0.29	0.05
Laportea alatipes	rt	0.24	0.05
Carduus kikuyorum	st	0.06	0.04
Crassocephalum ducis-aprutii	st	0.63	0.03
Vernonia adolfi-fredricii	pi	0.09	0.03
Carduus leptocanthus	lf	0.03	0.02
Discopodium penninervium	pi	0.02	0.02
Crassocephalum ducis-aprutii	rt	0.11	0.01
Peucedanum linderi	rt	0.05	0.01
Arundinaria alpina	sh	0.05	0.01
Carduus leptocanthus	st	0.04	0.01
Rumex rwenzorienses	st	0.03	0.01
Lobelia giberroa	rt	0.02	0.01
Dead stems opened[1]		1.08	
Rubus spp.	st	0.60	
Senecio johnstonii	rt	0.43	

[1] apparently to obtain insect cocoons or egg cases.

Table 4.6a, continued.

Species	Part	Frequency	Biomass
Lobelia stuhlmanii	rt	0.28	
Lobelia stuhlmanii	lf	0.25	
Vernonia adolfi-fredricii	fl	0.19	
Plectranthus laxiflorus	lf	0.16	
Vine sp. A	lf	0.15	
Gynura scandens	lf	0.13	
Hypericum revolutum	dw	0.12	
Vernonia adolfi-fredricii	tw	0.12	
Vine sp. A	cu	0.08	
Cineraria deltoidea	lf	0.08	
Oreosyce africana	lf	0.08	
Vernonia adolfi-fredricii	lf	0.08	
Hagenia abyssinica	dw	0.07	
Clematis simensis	lf	0.06	
Arundinaria alpina	lf	0.05	
Prenanthes subpeltata	lf	0.05	
Hagenia abyssinica	ba	0.04	
Lobelia stuhlmanii	ba	0.04	
Lobelia giberroa	pi	0.04	
Cinereria deltoidea	st	0.04	
Peucedanum kerstenii	st	0.04	
Carduus nyassanus	fl	0.03	
Hypericum revolutum	ba	0.02	
Galium spp.	cu	0.02	
Urtica massaica	rt	0.02	
Plectranthus laxiflorus	st	0.02	
Pygeum africanum	ba	0.01	
Prenanthes subpeltata	cu	0.01	
Carduus kikuyorum	fl	0.01	
Echinops hoehlenii	fl	0.01	
Helichrysum sp.	lf	0.01	
Stephania abyssinica	lf	0.01	
Carduus leptocanthus	rt	0.01	
Senecio sp.	st	0.01	

Table 4.6b. The relative frequency and biomass of all foods recorded in the diet of Group 11. See Table 4.6a for further explanation.

Species	Part	Frequency	Biomass
Galium spp.	ls	31.66	53.12
Carduus leptocanthus	rt	4.02	10.50
Vernonia auriculifera	pi	4.84	6.89
Basella alba	lf	16.06	5.07
Peucedanum linderi	st	4.42	4.87
Arundinaria alpina	lf	1.34	3.32
Arundinaria alpina	sh	8.60	2.99
Droguetia iners	lf	7.66	2.92
Carduus leptocanthus	lf	3.26	2.64
Rubus spp.	lf	0.76	2.04
Carduus leptocanthus	st	2.06	1.34
Urera hypselodendron	cu	1.41	1.16
Discopodium penninervium	pi	0.78	0.61
Urera hypselodendron	lf	1.16	0.53
Fungus sp.	fu	0.03	0.44
Tacazzea apiculata	cu	0.25	0.25
Carduus kikuyorum	lf	0.15	0.23
Cynoglossum spp.	rt	0.45	0.18
Urtica massaica	st	0.44	0.18
Laportea alatipes	lf	0.72	0.16
Carduus kikuyorum	st	0.13	0.10
Carduus kikuyorum	rt	0.13	0.09
Carduus nyassanus	lf	0.05	0.09
Lobelia giberroa	rt	0.06	0.06
Carduus nyassanus	rt	0.03	0.05
Coccinea mildbraedii	fr	0.13	0.04
Vernonia adolfi-fredricii	pi	0.07	0.03
Laportea alatipes	st	0.12	0.02
Crassocephalum ducis-aprutii	rt	0.07	0.02
Carduus nyassanus	st	0.04	0.02
Vine sp. A	cu	0.12	0.01
Galium spp.	cu	0.07	0.01
Peucedanum linderi	rt	0.04	0.01
Cyanoglossum spp.	st	0.03	0.01
Mikania capensis	lf	3.05	
Oreosyce africana	lf	0.96	
Discopodium penninervium	fr	0.66	

Table 4.6b, continued.

Species	Part	Frequency	Biomass
Helichrysum maraguensis	lf	0.63	
Tacazzea apiculata	lf	0.37	
Vine sp. A	lf	0.34	
Carduus leptocanthus	fl	0.33	
Clematis simensis	lf	0.33	
Vernonia sp.	lf	0.27	
Dead stem opened[1]		0.24	
Lagenaria abyssinica	lf	0.23	
Plectranthus laxiflorus	lf	0.17	
Stephania abyssinica	lf	0.16	
Geranium aculeolatum	lf	0.11	
Mikaniopsis clematoides	lf	0.11	
Rubus spp.	st	0.07	
Tinospora caffra	lf	0.07	
Vine sp. B	lf	0.07	
Ants		0.06	
Dombeya goetzenii	ba	0.06	
Lactuca glandulifera	lf	0.06	
Cineraria deltoidea	lf	0.05	
Coccinea mildbraedii	lf	0.05	
Clerodendron johnstonii	lf	0.04	
Vernonia auriculifera	tw	0.04	
Acalypha psilostachya	lf	0.03	
Hypericum revolutum	dw	0.03	
Vine sp. C	lf	0.03	
Vernonia auriculifera	ba	0.02	
Vernonia auriculifera	lf	0.02	
Discopodium penninervium	lf	0.01	
Dombeya goetzenii	lf	0.01	
Galiniera coffeoides	lf	0.01	
Galiniera coffeoides	st	0.01	
Hagenia abyssinica	ba	0.01	
Herb sp.	cu	0.01	
Herb sp.	lf	0.01	
Laportea alatipes	rt	0.01	
Vernonia adolfi-fredricii	lf	0.01	
Vernonia adolfi-fredricii	rt	0.01	

[1] apparently to obtain insect cocoons or egg cases.

Figure 4.1. The relative biomass of the main food items in the diets of Beetsme's group and Group 11. Foods contributing ≥ 1 % to the diet of either group are included. See Table 4.6 for full species names and key to plant parts.

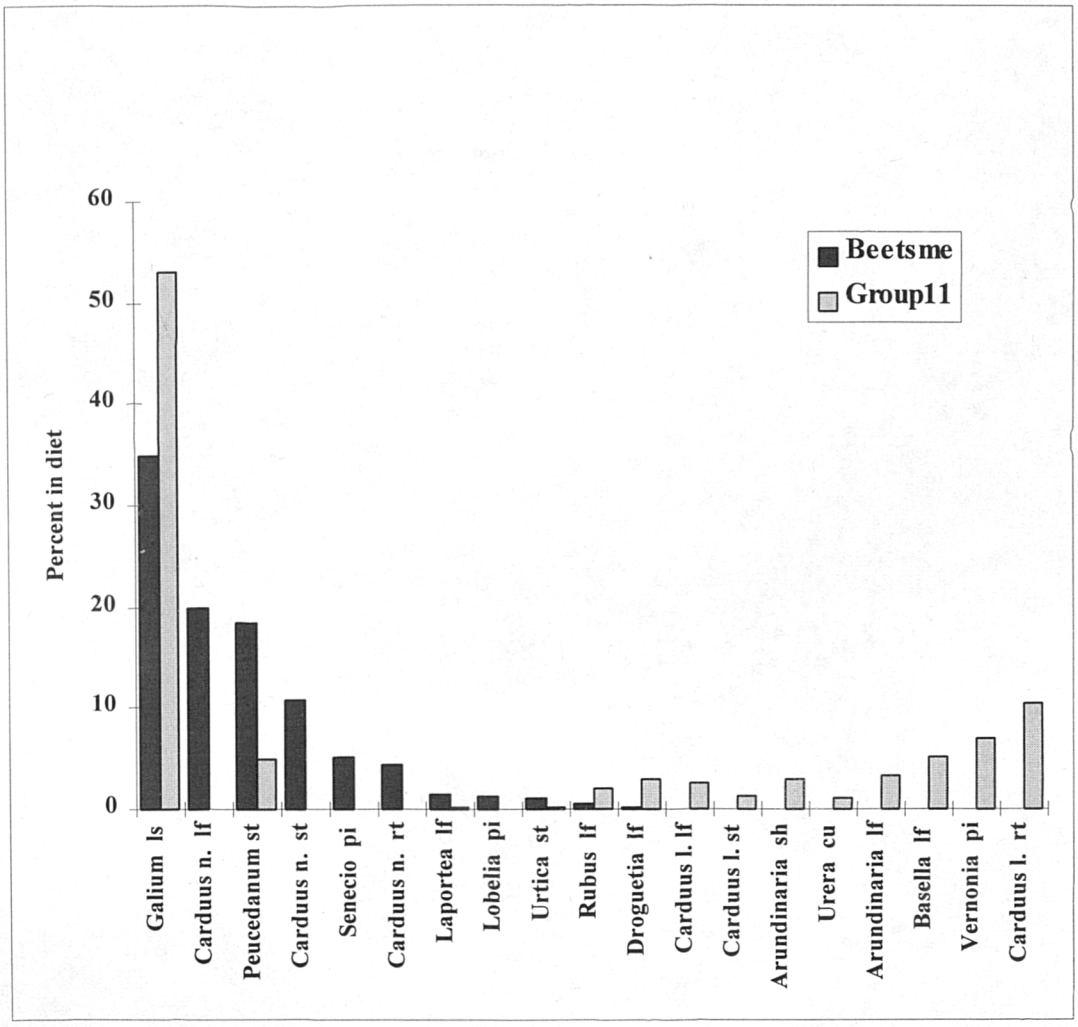
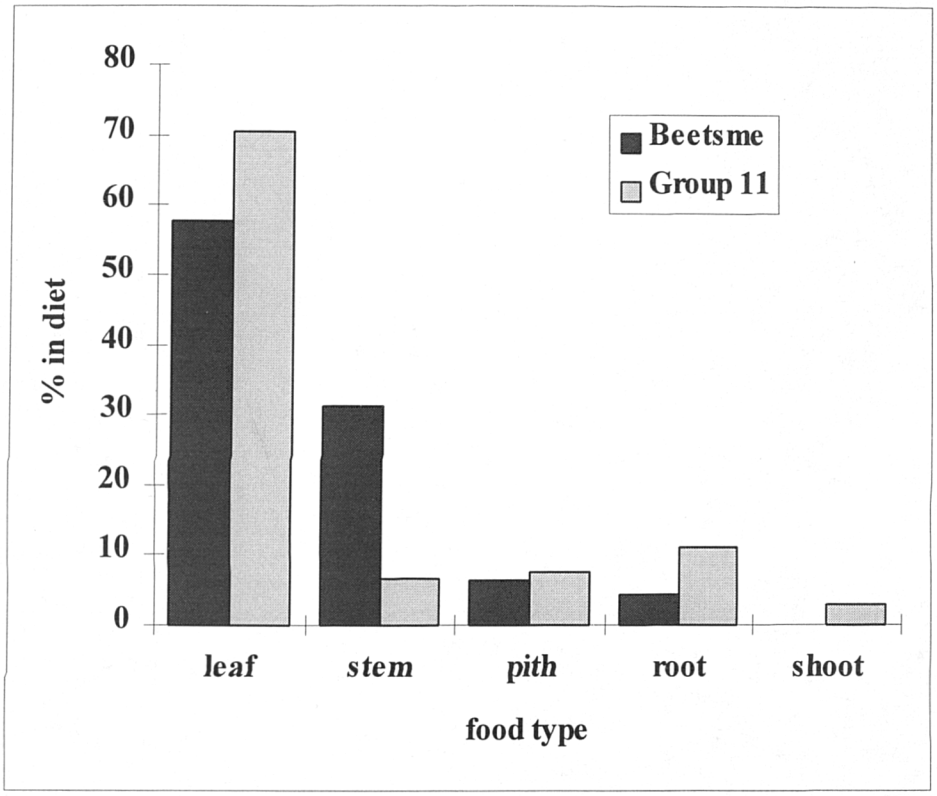


Figure 4.2. The relative biomass of the main food types in the diets of Beetsme's group and Group 11.



Beetsme's group were herbaceous plants such as *C. nyassanus* and *P. linderi*, the stems of which were peeled and eaten, while Group 11 ate more leaves from vines, including *Galium* spp. and *Basella alba*.

Figure 4.3 shows rank/biomass histograms of the diets of the two groups. The shape of both graphs indicates that most of the diet is made up of a small number of species. The top three ranking foods comprised 73.4 % of the diet of Beetsme's group and 70.5 % of Group 11's diet, while the figures for the top ten foods were 98.0 % and 91.4 % respectively. A particularly large proportion (53.1 %) of the Group 11's diet was made up of the highest ranking food (*Galium* spp.).

The dietary diversities of the two groups were equal when calculated using the Shannon-Wiener index from the relative biomass of foods in the diet (Table 4.7). The Simpson index, however, was lower for Group 11 than for Beetsme's group. This difference reflects the large biomass of the highest ranking food in the diet of Group 11. The Simpson index is as a dominance measure, and is more heavily weighted by the most abundant species than the Shannon-Wiener index (Magurran, 1988). Such diversity indices reflect both the number of species and the evenness, or equitability, of their contributions to, in this case, the diet of the two groups. The number of food items in the diet of Group 11 (72) was 9.0 % greater than in the diet of Beetsme's group (65). With the dominance of the highest ranking food in the diet of Group 11, the evenness of Group 11's diet is lower, reflected in a slightly lower equitability (Table 4.7).

The trail signs data allowed the number of species and number of food items consumed per day to be calculated for the two groups. Group 11 ate more food items (median 15) from more species (median 12) per day than Beetsme's group (median 11 foods and 8 species). These differences were statistically significant (Mann-Whitney $U = 808$, $p < 0.001$ and $U = 400$, $p < 0.001$ respectively,

Figure 4.3. Rank/biomass histograms of foods in the diets of Beetsme's group and Group 11. All food items for which biomass estimates could be made from either trail signs or faecal analysis are included (n = 29 for Beetsme's group and n = 34 for Group 11).

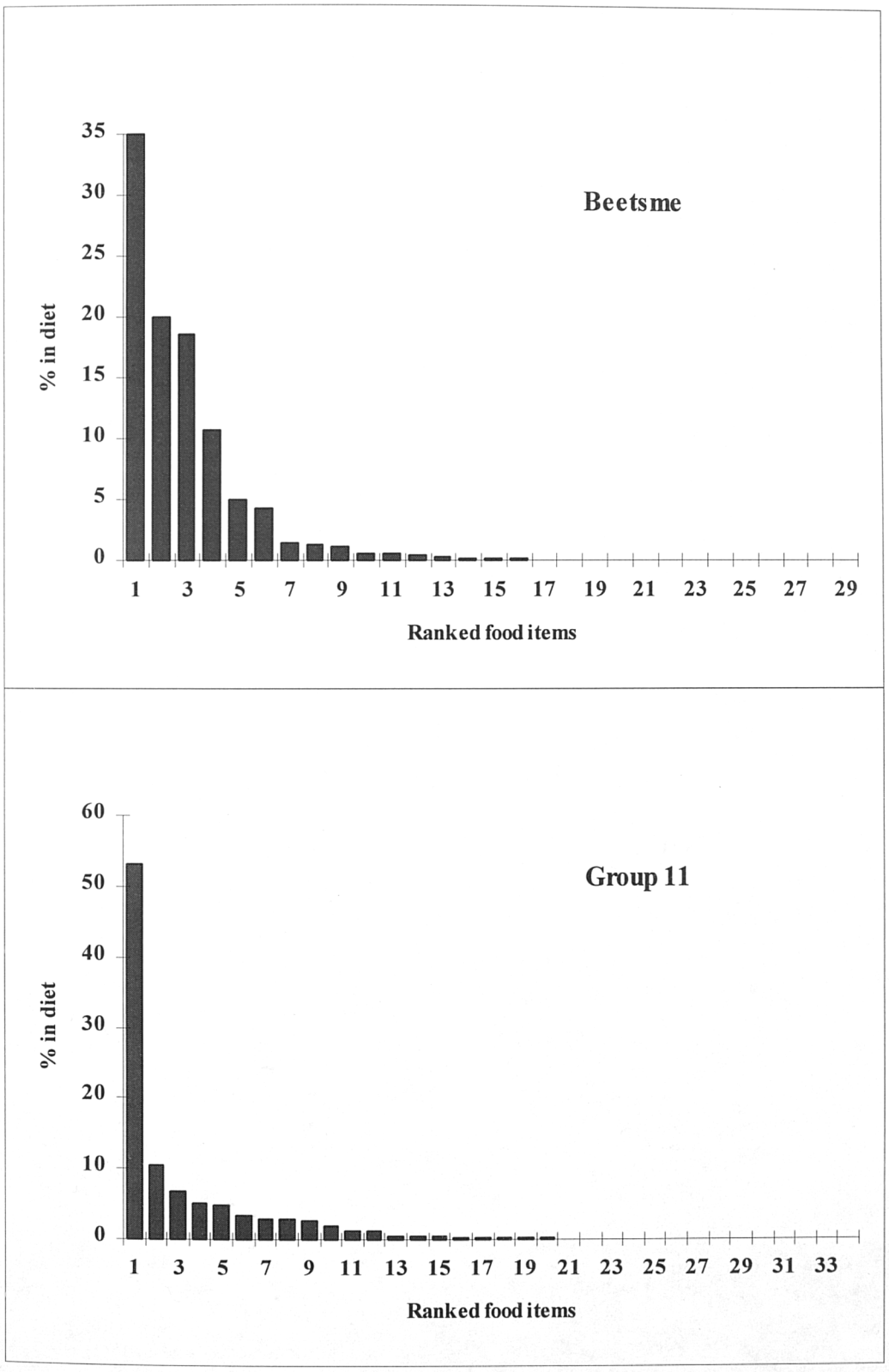


Table 4.7. The diversity and equitability of the diets of Beetsme's group and Group 11. Both Simpson's and Shannon-Wiener indices are given, calculated from the relative biomass of foods in the diet.

Index	Beetsme's group	Group 11
Simpson,	4.70	3.25
Shannon-Wiener,	1.85	1.85
equitability	0.55	0.52

n = 53 for Group 11 and n = 59 for Beetsme's group). In addition to a slightly broader overall diet, Group 11 thus had a broader diet on a daily basis than Beetsme's group.

Seeds of *Galium* spp. and *Rubus* spp. fruits were found in the faeces of both groups, while *Discopodium penninervium* seeds were found only in samples from Group 11. Figure 4.4 shows the numbers of each found for the two groups. Significantly more *Galium* spp. seeds were found in faecal samples from Group 11 (Mann-Whitney U = 670.5, $p < 0.001$, n = 64 for Beetsme's group and 61 for Group 11), but the difference in numbers of *Rubus* spp. seeds was not significant (U = 1897). Fragments of driver ants were found in 72 % (n = 44) of faecal samples from Group 11, but none of those from Beetsme's group. Signs of ant eating were found 5 times on the trails of Group 11.

4.3.5 Selectivity and preference

In order to compare the degree to which the two groups fed selectively, Ivlev's electivity index was used to measure the selection of each food relative to its availability by each group. Manly's alpha (Chesson, 1983) was used as a measure of preference, where preference is defined as the degree to which each food is selected relative to the degree to which all other foods are selected and reflects the proportion of the diet that would consist of each food if all foods were equally abundant in the environment (Johnson, 1980). The formulae for the two indices are *as follows:*

Ivlev's electivity index = $(r_i-n_i)/(r_i+n_i)$

Manly's alpha = $(r_i/n_i)/\Sigma(r_j/n_j)$

where r_i, r_j = proportions of food types i and j in the diet

n_i, n_j = proportions of food types i and j in the home range

j = 1,2,3...m

m = total number of food types

Ivlev's index gives a value between -1 and 1, reflecting the size of the difference between the availability and use of each food item, positive values indicating a greater proportion in the diet than expected on the basis of availability, i.e. a positive selection of that food. Manly's alpha gives values between 0 and 1 which sum to unity. If all foods are selected equally, Manly's alpha gives equal values for each, i.e. 1/m. Values greater than this indicate a preference.

The relative biomass of each food in the home range was calculated using the density estimates for each habitat type described in Chapter 2 and the area of each habitat within the minimum convex polygon home ranges, based on the mid-points of the trails of each group and described in Chapter 3. The ranging data used were collected over the same time period as the dietary data described in this chapter. Estimates of the biomass of some of the less common foods were not possible during the vegetation surveys and others were not found within any of the sample plots. Selection and preference indices could not therefore be calculated for all foods. Those indices which were calculated are given in Table 4.8. In order to compare like with like for the two groups, the indices were also calculated using only those foods which comprised more than 1 % of the diet of the group concerned (Table 4.9). Biomass estimates were available for all such foods. Rare foods

Figure 4.4. The mean number of seeds of each species found in faecal samples from Beetsme's group and Group 11. Approximately equal quantities of faeces were collected each day.

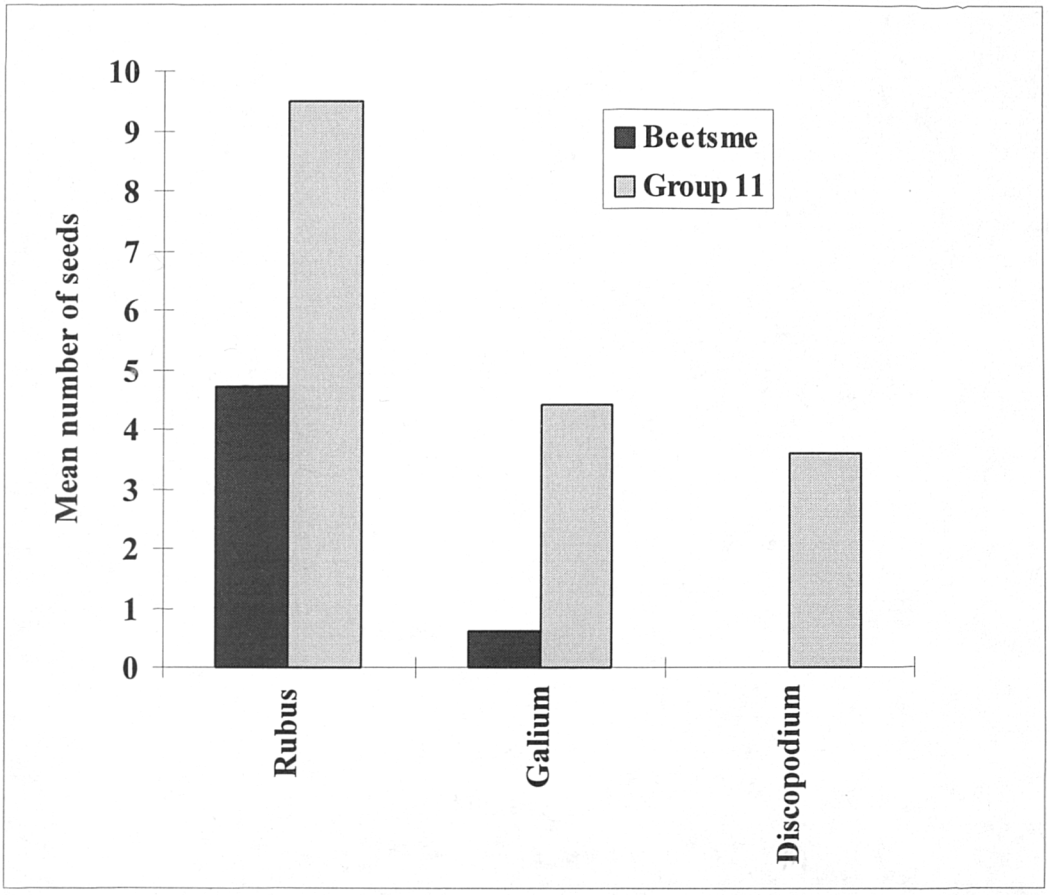


Table 4.8a. The relative biomass of foods in the diet and home range of Beetsme's group, with Ivlev's electivity index and Manly's alpha as a measure of preference. Values of Ivlev's index which indicate positively selected foods and of Manly's alpha which indicate a preferred food are shown in bold. All foods for which biomass estimates in the diet could be made are listed. However, estimates of biomass in the home range, and therefore of the two indices, were not possible in every case. See Table 4.6 for key to plant parts and text for further explanation.

Species	Part	Percent in diet	Percent in range	Ivlev	Manly
Galium spp.	ls	34.96	9.73	**0.565**	**0.079**
Carduus nyassanus	lf	19.94	11.78	**0.257**	0.037
Peucedanum linderi	st	18.54	6.41	**0.486**	**0.064**
Carduus nyassanus	st	10.72	3.81	**0.476**	**0.062**
Senecio johnstonii	pi	5.07	1.82	**0.471**	**0.061**
Carduus nyassanus	rt	4.31	3.26	**0.139**	0.029
Laportea alatipes	lf	1.39	10.36	-0.763	0.003
Lobelia stuhlmanii	pi	1.28	0.69	**0.298**	0.041
Urtica massaica	st	1.14	2.23	-0.323	0.011
Laportea alatipes	st	0.64	40.93	-0.969	0.000
Rubus spp.	lf	0.60	1.52	-0.435	0.009
Helichrysum formosissimum	lf	0.41			
Carex bequaertii	lb	0.23	0.01	**0.925**	**0.568**
Cyperus mannii	lf	0.20	6.16	-0.937	0.001
Droguetia iners	lf	0.14	0.21	-0.208	0.014
Carduus kikuyorum	lf	0.12			
Cyperus mannii	lb	0.05	0.34	-0.746	0.003
Laportea alatipes	rt	0.05			
Carduus kikuyorum	st	0.04			
Crassocephalum ducis-aprutii	st	0.03			
Vernonia adolfi-fredricii	pi	0.03	0.07	-0.393	0.010
Carduus leptocanthus	lf	0.02			
Discopodium penninervium	pi	0.02	0.07	-0.566	0.006
Crassocephalum ducis-aprutii	rt	0.01			
Peucedanum linderi	rt	0.01			
Arundinaria alpina	sh	0.01			
Carduus leptocanthus	st	0.01			
Rumex rwenzorienses	st	0.01	0.58	-0.966	0.000
Lobelia giberroa	rt	0.01			

Table 4.8b. The relative biomass of foods in the diet and home range of Group 11, with Ivlev's electivity index and Manly's alpha as a measure of preference. See Table 4.8a for further explanation.

Species	Part	Percent in diet	Percent in range	Ivlev	Manly
Galium spp.	ls	53.12	7.37	**0.756**	0.044
Carduus leptocanthus	rt	10.50	0.11	**0.979**	**0.581**
Vernonia auriculifera	pi	6.89	0.75	**0.803**	**0.056**
Basella alba	lf	5.07	0.92	**0.692**	0.034
Peucedanum linderi	st	4.87	2.91	**0.252**	0.010
Arundinaria alpina	lf	3.32	33.47	-0.820	0.001
Arundinaria alpina	sh	2.99	0.71	**0.616**	0.026
Droguetia iners	lf	2.92	3.48	-0.088	0.005
Carduus leptocanthus	lf	2.64	0.12	**0.915**	**0.139**
Rubus spp.	lf	2.04	1.35	**0.205**	0.009
Carduus leptocanthus	st	1.34	0.11	**0.847**	**0.074**
Urera hypselodendron	cu	1.16	3.76	-0.529	0.002
Discopodium penninervium	pi	0.61	2.75	-0.637	0.001
Urera hypselodendron	lf	0.53	1.99	-0.579	0.002
Fungus sp.	fu	0.44			
Tacazzea apiculata	cu	0.25			
Carduus kikuyorum	lf	0.23			
Cynoglossum spp.	rt	0.18			
Urtica massaica	st	0.18	19.94	-0.982	0.000
Laportea alatipes	lf	0.16	3.42	-0.911	0.000
Carduus kikuyorum	st	0.10			
Carduus kikuyorum	rt	0.09			
Carduus nyassanus	lf	0.09	2.09	-0.917	0.000
Lobelia giberroa	rt	0.06			
Carduus nyassanus	rt	0.05	0.61	-0.849	0.001
Coccinea mildbraedii	fr	0.04			
Vernonia adolfi-fredricii	pi	0.03	0.01	**0.400**	0.014
Laportea alatipes	st	0.02	13.24	-0.997	0.000
Crassocephalum ducis-aprutii	rt	0.02			
Carduus nyassanus	st	0.02	0.65	-0.940	0.000
Vine sp. A	cu	0.01	0.23	-0.917	0.000
Galium spp.	cu	0.01			
Peucedanum linderi	rt	0.01			
Cynoglossum spp.	st	0.01			

Table 4.9. The relative biomass of the principle foods in the diet and home range of the two study groups, with Ivlev's electivity index and Manly's alpha as a measure of preference. Values of Ivlev's index which indicate positively selected foods and of Manly's alpha which indicate a preferred food are shown in bold. Only foods comprising more than one percent of the diet are included. The percentage in the diet and home range are calculated using only these species and so differ from the values given in Table 4.8. See Table 4.6 for key to plant parts and text for further explanation.

Species	Part	Percent in diet	Percent in range	Ivlev	Manly
Beetsme's group					
Galium spp.	ls	35.91	19.42	**0.298**	**0.204**
Carduus nyassanus	lf	20.48	23.52	-0.069	0.096
Peucedanum linderi	st	19.04	12.80	**0.196**	**0.164**
Carduus nyassanus	st	11.01	7.61	**0.184**	**0.160**
Senecio johnstonii	pi	5.21	3.63	**0.177**	**0.158**
Carduus nyassanus	rt	4.43	6.51	-0.190	0.075
Laportea alatipes	lf	1.43	20.68	-0.871	0.008
Lobelia stuhlmanii	pi	1.31	1.38	-0.025	0.105
Urtica massaica	st	1.17	4.45	-0.583	0.029
Group 11					
Galium spp.	ls	54.84	13.39	**0.607**	0.045
Carduus leptocanthus	rt	10.84	0.20	**0.963**	**0.592**
Vernonia auriculifera	pi	7.11	1.36	**0.677**	0.057
Basella alba	lf	5.23	1.67	**0.514**	0.034
Peucedanum linderi	st	5.03	5.28	-0.025	0.010
Arundinaria alpina	lf	3.43	60.79	-0.893	0.001
Arundinaria alpina	sh	3.09	1.29	**0.410**	0.026
Droguetia iners	lf	3.01	6.32	-0.355	0.005
Carduus leptocanthus	lf	2.73	0.22	**0.855**	**0.141**
Rubus spp.	lf	2.11	2.45	-0.075	0.009
Carduus leptocanthus	st	1.38	0.20	**0.745**	0.076
Urera hypselodendron	cu	1.20	6.83	-0.702	0.002

provide poor opportunities for measuring preference (Chesson, 1983) and little emphasis should be put on the values obtained for such foods.

Both groups showed a comparable pattern of selectivity in the proportions of food in their diets. Certain foods, such as *Galium* spp., *C. nyassanus* and *Carex bequaertii* for Beetsme's group and *Galium* spp. and *Carduus leptocanthus* for Group 11 were positively selected, and others such as *U. massaica* and *L. alatipes* stems were avoided by both groups, giving low values of Ivlev's index. As the data were collected using two different techniques and do not represent repeated samples, statistical analysis of this selectivity was not possible. However, the Ivlev's values are clearly different from the column of zeros that would be expected if feeding was non-selective and therefore in proportion to availability.

Both groups showed a preference for a small number of foods. The values of Manly's alpha for Group 11's diet were greatly affected by the fact that they ate a large proportion of *C. leptocanthus* roots, stem and leaves, which were rare in their home range. In fact only one small *C. leptocanthus* plant was found in one of the 68 vegetation sampling plots in the main habitat type in their range, *Mimulopsis*. This plant shows a clumped distribution and the biomass estimates could be inaccurate. However, the biomass of these food items was undoubtedly small, indicating a high preference given the relatively large proportions in the diet. In addition the biomass estimate of bamboo (*A. alpina*) leaves was very high. Although the distinction could not be made from faecal analysis, the gorillas generally ate leaves from young stems. This would make the effective availability considerably lower, so that the relative biomass of other foods would be proportionally higher. However, the general pattern of preference for a small number of foods was clear despite these problems.

4.4 DISCUSSION

4.4.1 Accuracy of trail signs and faecal analysis

The two indirect methods of sampling diet, faecal analysis and trail signs, both gave results which were in good agreement with the direct observations of feeding behaviour. The main problem was that neither method included all possible food types. In this study, it was possible to combine data from the two types with reference to the observations and frequency measures that were made, but such a cross-check might not always be possible. This study, unlike those of Plumptre (1991) and Norbury (1988), found that the results from faecal analysis were not significantly improved by correcting for the proportion of cuticle which was unidentifiable for each plant species. However both Norbury (1988) and Plumptre (1991) used a different range of plants, including grasses, and this correction should still be considered given their findings. A further disadvantage of faecal analysis is that different ages of leaves cannot easily be distinguished. However, this study has shown that the technique can be effective in identifying important food items, especially where the diet consists mostly of leaves.

4.4.2 Dietary variation within the Virungas

The overall dietary patterns of both groups were in agreement with previous findings that mountain gorillas in the Virungas are primarily folivorous and show considerable specialisation on plant parts and species (Watts, 1984; Plumptre, 1991, 1995). The two study groups did each consume a different array of foods. Watts (1984) found that the diet of one group varied markedly with spatial variability in habitat, variation between groups occupying different habitats would thus be expected. Both study groups fed selectively, in agreement with predictions that

large herbivores should feed so as to obtain an optimal nutrient mix, while avoiding deleterious levels of plant secondary compounds (Westoby, 1974; Altmann & Wagner, 1977; Watts, 1984).

Although the dietary diversities of the two groups were similar, Group 11 was found to have a broader diet on a daily basis than Beetsme's group and a slightly broader overall diet. The response of the gorillas to areas of lower food abundance than the Karisoke study area was thus a combination of broadening of the diet, and travelling further per day and between feeding sites as described in Chapter 3. Both these responses would be predicted by foraging theory as ways in which to increase foraging efficiency in response to reduced food availability (Schoener, 1971; Vedder, 1984). The broadening of the diet suggests that the increased search costs associated with travelling further were sufficiently large to warrant including more food items in the diet.

While Group 11, ranging in a lower altitude region of the Virungas, did show differences in diet from Beetsme's group in the Karisoke study site, these differences were not as large as those between the Virungas and other gorilla populations. For instance, eastern lowland gorillas in Zaire have been reported to eat 160 food items from 78 plant species (Goodall, 1977) while western lowland gorillas in Gabon included 182 foods from 134 species. There was little evidence that fruits played a large part in Group 11's diet. Few signs indicating fruit consumption were found along their trails, although these were easier to miss than signs of feeding on leaves and stems. There were, however, more seeds in the faecal samples from Group 11 than those from Beetsme's group. The guides following the lowest group of gorillas on the Zairean side of the Virungas (Ndungutsi's group, see Chapter 3) pointed out 13 plant species from which they had seen gorillas eat fruit, 10 of which were not found in the Karisoke site and 7 of which were not found even in Group 11's range. Several of the species eaten by

Group 11 but not by Beetsme's group, notably *Basella alba* and *Urera hypselodendron*, were recorded as important foods in the diet of eastern lowland gorillas (Casimir, 1975; Goodall, 1977) as were many of the foods reported to be eaten on the Zairean side of the Virungas. These observations do suggest that the diet of the lower groups in the Virungas resemble that in other populations more closely than that of the Karisoke study groups, probably including a greater proportion of fruit in the diet. A detailed investigation of the diet in one of the lowest groups on the Zairean side of the Virungas would be necessary to confirm this.

The nutrient content and presence of plant secondary compounds is likely to be one of the most important determinants of dietary selection (Waterman, 1984). Protein content and digestibility have been found to influence selection of foods by in western lowland gorillas (Calvert, 1985; Rogers *et al.*, 1990). Plumptre (1995) and Watts (1983) both undertook nutritional analysis of food plants eaten by gorillas in the Karisoke study area and found that in vitro digestibility was the only measure which explained any of the pattern of selectivity. Neither study included energy content of foods, and Plumptre (1995) suggests this might be important. Further detailed study of dietary selection in relation to availability and more comprehensive analysis of food quality is needed before the factors underlying food selection will be fully understood.

Watts (1984) found that bamboo shoots were the only common food that was available and consumed seasonally. Plumptre (1991) found evidence of seasonality in the diet, but attributed this to the movement patterns of the gorilla groups. Some areas were not visited during a particular season, causing seasonal differences in the consumption of foods found there, which would not necessarily be consistent from year to year. Seasonal variation in diet was not analysed in this study, which was concerned primarily with overall variation in dietary patterns between groups. For

example, in order to compare the importance of bamboo shoots in the diet relative to other food items, the most meaningful comparison would be between overall annual means.

The differences observed between the two main study groups, both in terms of the actual foods and food types eaten and in terms of dietary breadth, indicate a degree of adaptability in the diet of the gorillas. As has been seen in Chapters 2 and 3, they are able to utilise most habitat types, covering a large part of the altitudinal range of the Virungas. Having considered the effects of variation in food availability at the levels of home ranges, habitats used and foods eaten, the influence of human disturbance on the gorilla population will be addressed in the next chapter.

CHAPTER FIVE

THE EFFECTS OF HUMAN DISTURBANCE ON GORILLAS IN THE VIRUNGAS

5.1 INTRODUCTION

Debate on the causes of the decline in the Virunga gorilla population during the 1960s and 1970s has focussed on the relative importance of habitat loss and poaching and other forms of human disturbance within the park (Harcourt & Fossey, 1981; Weber & Vedder, 1983). Direct hunting of gorillas was prevalent during unrest in Zaire in the mid-1960s, and in response to a market for gorilla trophies and live young during the 1970s. Cattle were grazed in much of the forest until 1977. Although these severe forms of human disturbance no longer threatened the population, at least until the outbreak of civil war in Rwanda in 1990, illegal use of the forest continues. This disturbance takes the forms of hunting of antelope and hyrax for meat and skins, bamboo and other wood cutting, apiculture and smuggling (Aveling & Harcourt, 1984; *personal observation*).

Human disturbance could have a negative impact on the population in several ways. At the most direct level, gorillas can be caught in snares set for antelope. The individuals generally break free, leaving a noose around the hand or foot which can cause severe injuries and deaths, especially if made from wire. In 1991 alone, nine cases were reported of gorillas in monitored groups being caught in snares (Macfie, 1992). Human disturbance could also have less direct effects on the population. By effectively excluding the gorillas from certain areas, the area of suitable habitat available to the population would be reduced. Also, if chance encounters with illegal human users were frequent, this would cause stress to the gorillas. Unhabituated

groups generally flee from people (Sholley, 1991; *personal observation*), increasing energy expenditure and interrupting feeding. Poachers have been known to kill gorillas when encountered, even if they were not the intended quarry (Fossey, 1974), although this is not known to have occurred recently.

Several lines of evidence have indicated that human disturbance has a negative impact on the population. Previous studies have noted a difference in the gorilla population density and mean group size between the eastern section of the Virungas (Mounts Sabinyo, Gahinga and Muhavura) and the remainder (Fossey & Harcourt, 1977; Harcourt & Fossey, 1981; Harcourt *et al.*, 1981; Weber & Vedder, 1983). A higher level of human disturbance in this section has been suggested as a possible underlying cause (Fossey & Harcourt, 1977; Harcourt & Fossey, 1981), although Weber & Vedder (1983) indicated that differences in habitat quality could also be involved. In 1981 the section of the population on the Rwandan side of the Virungas contained a higher proportion of immatures than that on the Zaire side (Harcourt *et al.*, 1983). This indicates a healthier population and reflects the better protection afforded to the Rwandan side at that time (Aveling & Harcourt, 1984). By 1986, with improved protection on the Zaire side, the proportion of immatures there was as high as that in Rwanda (Aveling & Aveling, 1989).

There is also evidence that human disturbance has an impact on ranging patterns. Aveling & Aveling (1989) noted how several groups moved into areas which were previously heavily disturbed when these areas received improved protection. At a more detailed level, studies of individual groups in the Karisoke study area have found that avoidance of poaching risk influenced ranging behaviour (Fossey, 1974; Fossey & Harcourt, 1977; Watts, 1991).

Past censuses have all found considerable variation in the density of gorillas across the Virungas (Harcourt & Fossey, 1981; Weber & Vedder, 1983; Aveling &

Harcourt, 1984; Aveling & Aveling, 1989). As mentioned above the population density in the eastern section is lower than elsewhere. In addition very low densities of gorillas have been found in the section to the south of Mount Karisimbi, none having been found since 1981 (Aveling & Harcourt, 1984; C.R. Sholley and A. Vedder pers. comm.). As shown in Chapters 2 and 3, much of this area consists of habitat suitable for gorillas. Clearly factors other than habitat type influence the distribution of gorillas.

This study aimed to investigate the influence of illegal human disturbance on the gorillas use of available habitat in the Virungas. If disturbance was having a significant negative impact, gorillas would be expected to avoid areas where levels of disturbance were high. Two approaches were taken to this problem. Previous censuses of the population have not only noted the location and size of the gorilla groups, but also the presence of various signs of human disturbance (Harcourt & Fossey, 1981; Aveling & Harcourt, 1984). On a broad scale, this allowed the locations of gorilla groups to be compared with the distribution of signs of human disturbance. However, censuses do not represent systematic sampling of signs of human disturbance as the length of survey path walked per square kilometre varies considerably. Snares tend to be found in clumps and there may be considerable variation in the probability of particular snares being found. In addition, censuses provide only a 'snapshot' of the distribution of gorilla groups, without giving any indication of the relative use of different areas by them. In order to allow for these problems, systematic surveys of human disturbance and signs of gorilla use were made in a sample of sites across the range. It was predicted that the frequency of signs of gorillas would be inversely correlated with levels of illegal human disturbance.

5.2 METHODS

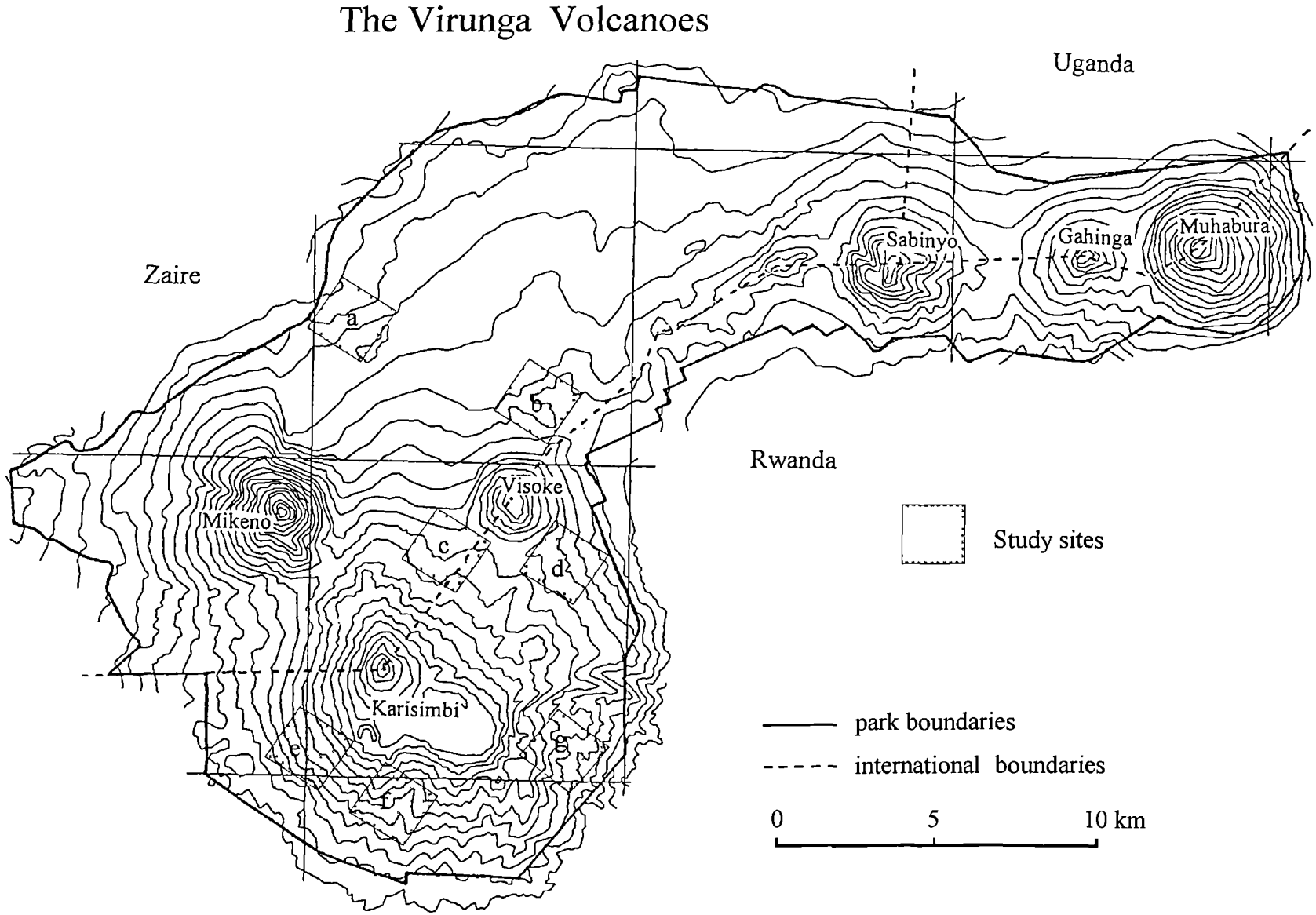
5.2.1 Census data

Raw data collected during the censuses undertaken in 1986 and 1989 were made available by A. Vedder and C.R. Sholley, to whom I am grateful. The methods used were the same in both (Sholley, 1991). An irregular network of trails was walked, the specific pattern of which was largely determined by terrain. When recent gorilla trail was found, it was followed to the sites of night nests, which allowed counts to be made of the size and composition of the group. The location of snares and other signs of human disturbance found during these surveys was noted on a 1 km^2 grid. In 1989, almost all census workers noted the location of snares, although other signs, such as trail of poachers, were recorded with less consistency. Unfortunately data on snares were available for less than 50 % of the area from the 1986 census, so these data were not used here. Data on the distribution of snares, the location of groups and the distance walked on survey trails were extracted from the original datasheets, maps and notebooks of the census workers.

5.2.2 Surveys of human disturbances and gorilla use

Six study sites, each 2 x 2 km, were selected along the accessible portion of the Rwandan side of the Virungas, with a seventh in Zaire (Figure 5.1). Habitats which were not used by gorillas (Alpine and Meadow, see Figure 2.2) were avoided. One edge of each site was measured and marked out as a baseline, and each was divided into four sections of 2 x 0.5 km. One randomly placed line transect was walked longwise through each section. The starting point of each transect was determined using random number tables. Four transects totalling approximately 8 km were thus walked in each of the seven study sites. Transect length was measured by pacing.

Figure 5.1. Study sites in which transect surveys of human disturbance and signs of gorilla use were made. Each site is distinguished by a letter, referred to in Table 4.1.


The Virunga Volcanoes
Uganda
Zaire
Rwanda
Sabinyo
Gahinga
Muhabura
Mikeno
Visoke
Karisimbi
a
b
c
d
e
f
g
Study sites
park boundaries
international boundaries
0
5
10 km

The exact length varied slightly due to terrain and time constraints, the minimum being 7.45 km and the maximum 8.03 km. For the sake of consistency, all transects were made outside the bamboo shooting season.

All snares and other signs of human disturbance seen along each transect were noted, and the vertical distance from the line to each was estimated. Distance estimations were checked periodically with a tape measure. The number of snares found in each site was insufficient for normal distance sampling procedures (Burnham *et al.*, 1980), but plotting the number of snares detected against distance from the line indicated that snares were reliably found within 5 m on either side. Each transect was therefore treated as a 10 m wide strip and data on snares seen outside this strip were not used in the analysis.

Gorillas leave clear trails as they move around the forest feeding, which are visible for several months. Human trails are also visible, although generally only for a few days. Each time the transect line crossed the visible trail of a poacher or other illegal user, or of a gorilla group, this was noted and the age of the sign estimated. Repeated signs of the same age which were clearly continuous trails and which were crossed within 200 m of each other on the same transect were not counted as separate trails. Experienced local trackers accompanied me on all transects, and when gorilla trails of known age were crossed, their age estimations were accurate. Trail of legal and illegal users of the forest could readily be distinguished by type of footwear and other characteristics. Comparisons were made of the ages of signs in the different sites, in order to compensate for differential rates of trail decay.

Estimates of the density of snares per km^2 were made for each site, along with the frequency of both gorilla and illegal human use, in terms of the number of trials crossed per km of transect. Spearman rank correlations were used to investigate the

relationships between gorilla use and the two indices of human disturbance. One-tailed tests were used as directional hypotheses were made.

5.3 RESULTS

5.3.1 The distribution of disturbance from census results

The locations of gorilla groups found during the 1989 census are shown in Figure 5.2, with larger groups indicated by larger circles. The majority of gorillas were found in the central section of the range, between Mounts Mikeno and Visoke in the west and Sabinyo in the east, with a smaller number in the eastern section. None were found in the area to the south and west of Karisimbi.

The distribution of snares found during the same census is shown in Figure 5.3, for those areas from which data were available (79 % of the total). Snares were found in a clumped distribution; none were found in the majority (88 %) of one kilometre squares, whereas a small number of squares contained many. Single snares were only found in eight squares. The area of highest snare density was clearly on Mount Mikeno, on the Zairean side of the range. Census workers' notes indicated that many of the snares found there were of a type set for hyrax which are not a threat to gorillas. However many antelope snares were also found there. Snares were also found in the eastern section of the Virungas and in the region to the south-west of Karisimbi. Only a small number were found in the central section.

The pattern suggests that the area in which most of the gorillas were found coincides with the area of lowest snare density, with the exception of Mikeno, on which five groups and one solitary male were found despite the high concentration of snares. For the sake of analysis, the region was divided into five sections, the eastern section

Figure 5.2. The locations of gorilla groups found during the 1989 census of the Virunga population. Group sizes (number of individuals) are distinguished by different sized circles.

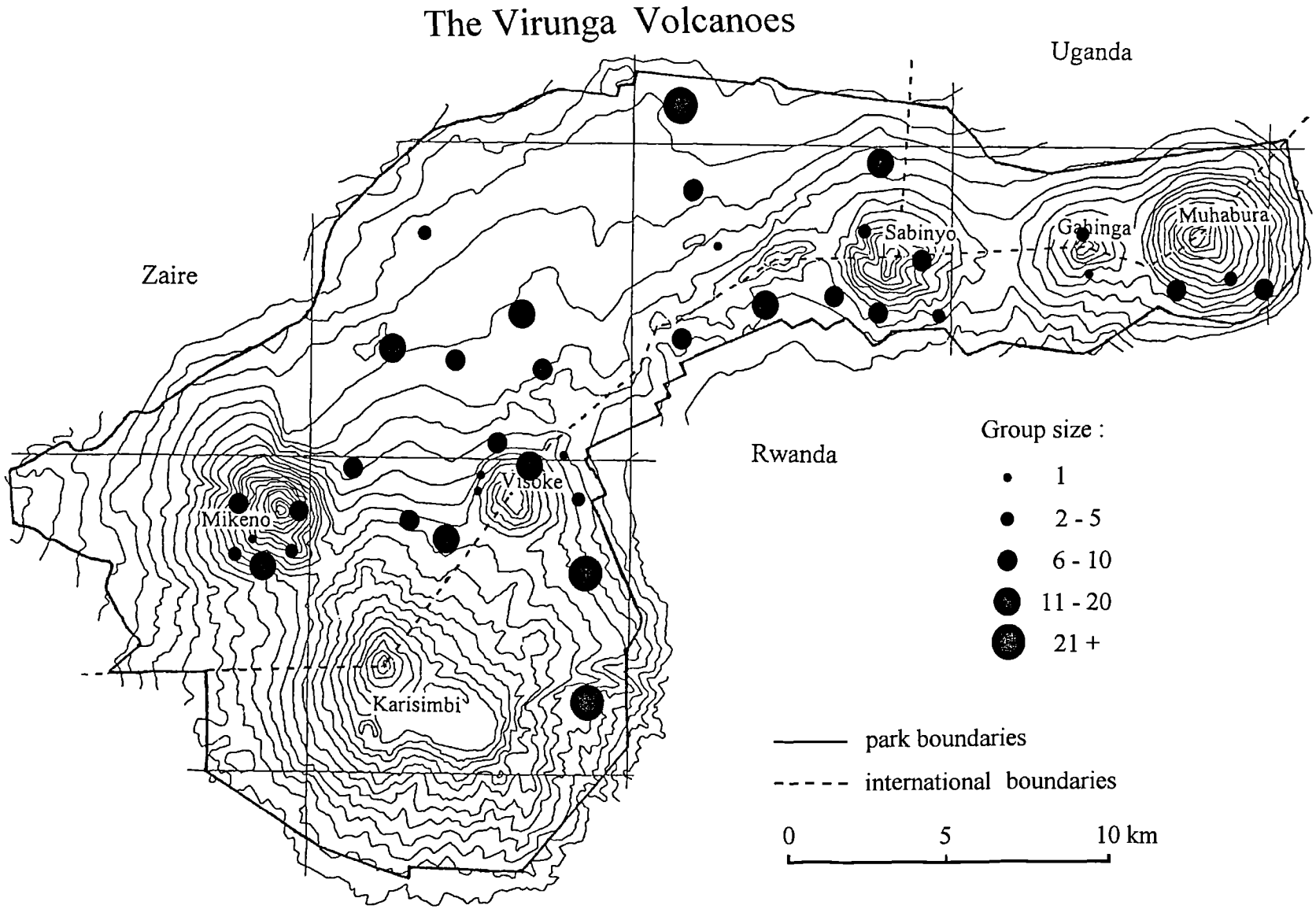
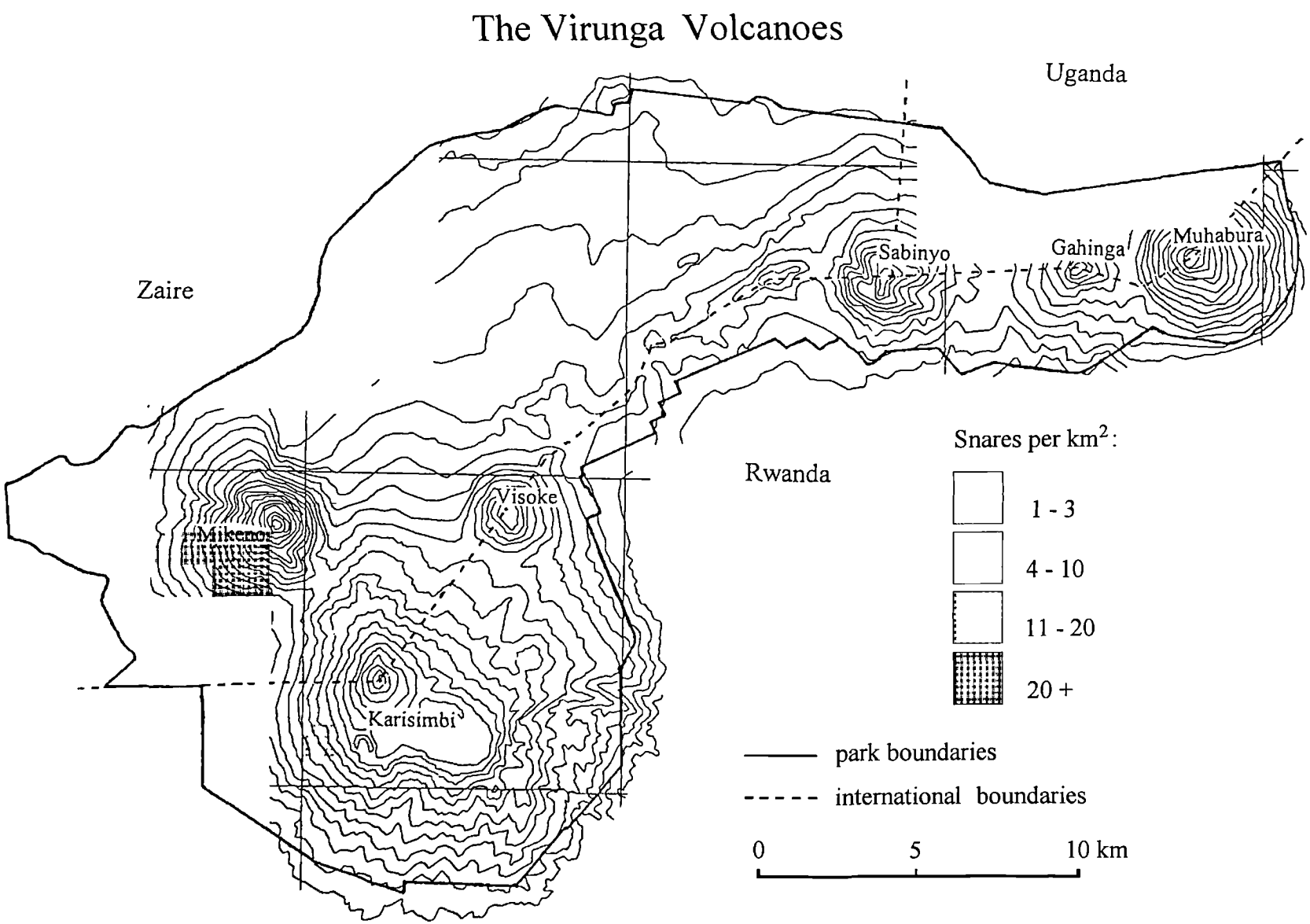

The Virunga Volcanoes
Uganda
Zaire
Rwanda
Sabinyo
Gahinga
Muhabura
Visoke
Mikeno
Karisimbi
Group size :
1
2 - 5
6 - 10
11 - 20
21 +
park boundaries
international boundaries
0
5
10 km

Figure 5.3. The distribution of snares in one kilometre squares found during the 1989 census of the Virungas. The areas of the map which are blanked out represent areas from which data on human disturbance were missing. Note that the length of survey trail walked per square varied considerably. Gross differences in the densities of snares in different areas are, however, clear.


The Virunga Volcanoes
Uganda
Zaire
Rwanda
Sabinyo
Gahinga
Muhabura
Visoke
Mikeno
Karisimbi
Snares per km2:
1 - 3
4 - 10
11 - 20
20 +
park boundaries
international boundaries
0
5
10 km

from Sabinyo eastwards; the central saddle section between Sabinyo, Mikeno and Visoke; the Karisoke section including the north side of Karisimbi and the whole of Visoke; the southern section to the south and west of Karisimbi; and lastly Mikeno. In order to compensate for the different lengths of survey trail walked in each area, the number of snares found was divided by the estimated total distance walked to give a measure of the number of snares encountered per km. As the census represents a complete count of the gorilla population, the density of gorillas was calculated from the number found in each section divided by the area of that section. The results are shown in Figure 5.4. There was no obvious relationship between the density of gorillas and the frequency with which snares were encountered.

5.3.2 Human disturbance and gorilla use

The age of gorilla signs varied between sites (Kruskal-Wallis, $H = 25.3$, $d.f. = 4$, $p < 0.001$). In order to compensate for differential rates of decay of gorilla trails, therefore, the number of trails crossed by transects was divided by the mean age of sign in each site. No significant differences were found in the age of signs of illegal human use between sites ($H = 8.46$, $d.f. = 6$, $p > 0.2$).

The results of the transect surveys of gorilla use and human disturbance are shown in Table 5.1. Signs of use by gorillas were found in all sites except the two on the south-western flanks of Karisimbi (South 1 and South 2). Signs of illegal human use were found in all sites, and snares were found in all except one. The estimated density of snares varied greatly between sites, from zero to 187 per km^2.

The relationships between gorilla use and the two indices of human disturbance are shown in Figure 5.5. The frequency of encounter of trails of illegal users was

Figure 5.4. The density of gorillas and the frequency with which snares were encountered per kilometre of survey trail walked during the 1989 census in the Virungas, divided into five sections as described in the text.

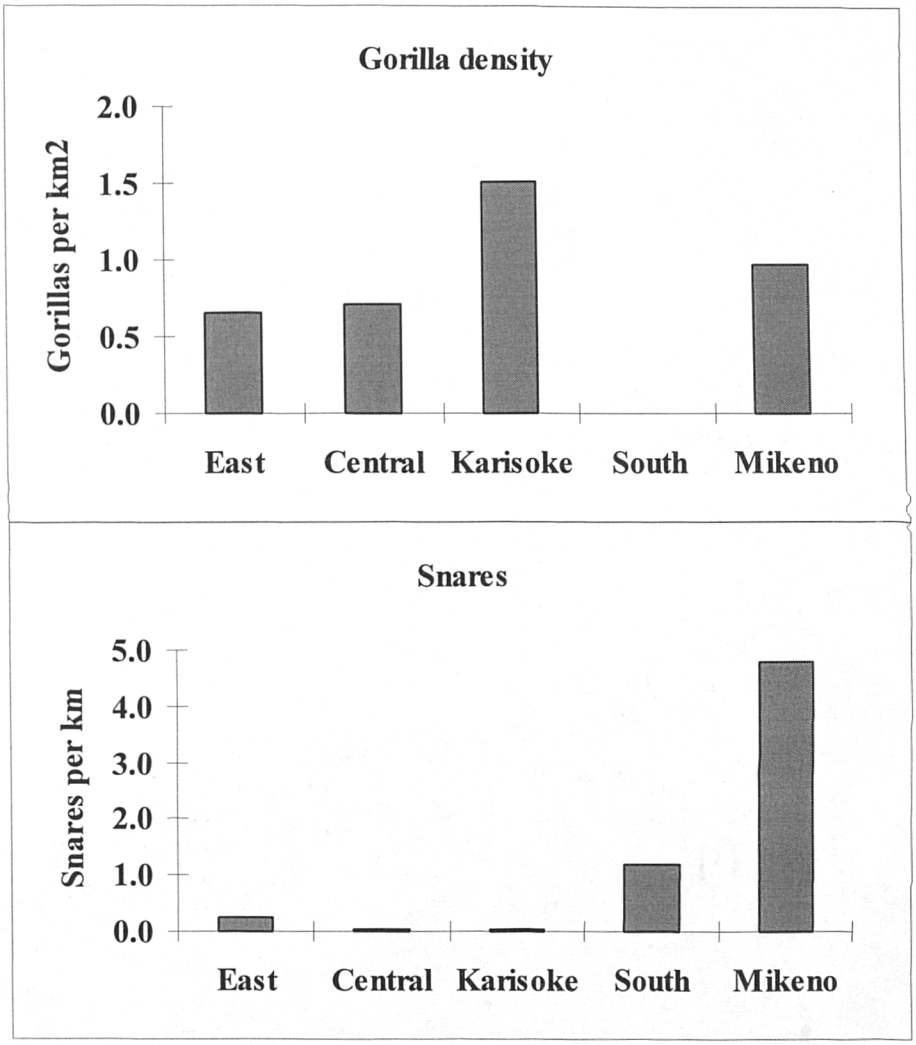
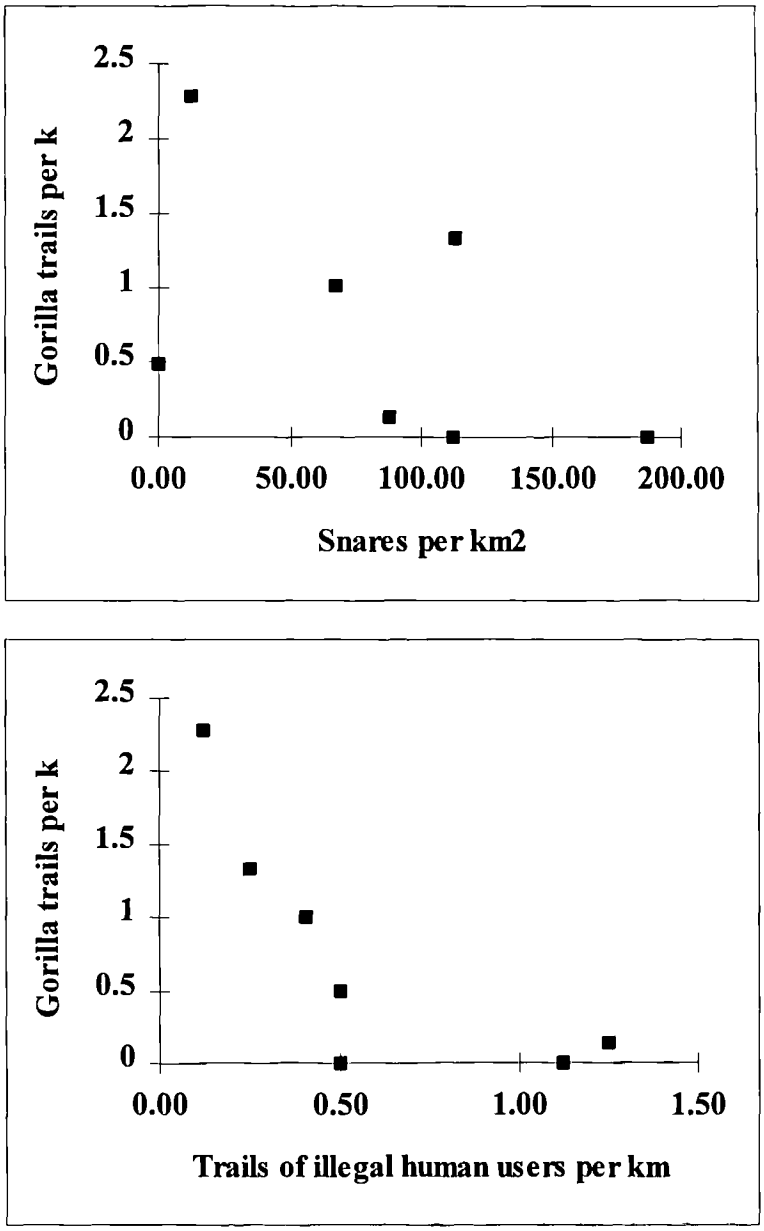


Table 5.1. The density of snares and the frequency of encountering signs of illegal human use and of gorillas in the seven study sites. The number of gorilla trails was divided by the mean age of trails in each site to compensate for differential rates of decay of trails.

Site	Gorilla trails per km	Human trails per km	Snare density per km^2	
A. Bukima	1.01	0.40	67.1	
B. Gisha	1.34	0.25	112.6	
C. Karisoke 1	0.49	0.5	0	
D. Karisoke 2	2.28	0.12	12.4	
E. South 1	0	1.12	187.2	
F. South 2	0	0.50	112.5	
G. Gashinga	0.14	1.25	87.5	

Figure 5.5. Scattergraphs showing the relationships between the frequency of encountering signs of gorilla use per kilometre of transect and the two indices of human disturbance. The indices are the estimated density of snares and the frequency of encounter of trail of illegal human users per km of transect. The number of gorilla trails was divided by the mean age of trails found in each site, in order to compensate for differences in the rate of decay of trails.



negatively correlated with gorilla use ($r_S = -0.79$, $p < 0.05$). The scattergraph suggests a weak negative correlation between snare density and gorilla use. This correlation, however, was not significant ($r_S = -0.47, p > 0.1$).

5.4 DISCUSSION

In the 1989 census, the majority of gorilla groups in the Virungas were found in the central section, from Sabinyo in the east to Visoke and Mikeno in the west. This coincides with the area in which fewest snares were found. Aside from this observation, there was no clear relationship between the density of gorillas and the frequency with which snares were found. Across the seven sites in which surveys of human disturbance were made in this study, signs of use by gorillas were inversely correlated with signs of human disturbance as predicted, but the results suggested only a weak (non-significant) inverse correlation between gorilla use and snare density.

Although an inverse correlation was established between gorilla use and human disturbance, this in itself does not prove a causal relationship. The five sites in which signs of gorillas were found were all situated within areas monitored by park personnel or research centre staff in the course of tourism or research. Such areas receive additional protection as a result of this monitoring. These activities only take place where gorillas are found, so that, in an indirect way, the presence of gorillas could result in fewer signs of illegal human disturbance. This could account, at least partly, for the inverse correlation found. When the analyses were restricted to the five monitored sites, any suggestion of a correlation between snare density and gorilla use disappeared ($r_S = 0.00$). This could reflect the fact that monitoring activities were most effective in removing snares. The correlation between gorilla use and signs of illegal human users, however, was still significant ($r_S = -1.00$, $p = 0.01$), indicating

that, even within areas which received additional protection as a result of the presence of gorillas, gorilla use was highest in areas of low levels of human disturbance.

If the distribution of snares is at least partly determined by the degree of protection, which is determined by research and tourism activities and thus depend on the presence of gorillas, this would explain the distribution of snares and gorilla groups found in the 1989 census. Tourism and research are concentrated in the central section of the range, where snares were encountered least. Although no tourism or research generally occurs either in the eastern section or on Mikeno, gorillas were found in both. More snares were found in these two areas. This supports the conclusion that the presence of snares alone does not greatly influence the distribution of gorillas, or their use of particular areas.

The inverse correlation found between signs of gorilla use and illegal human users supports the hypothesis that areas with high levels of human disturbance would be used less by gorillas relative to less disturbed areas. It can be concluded that disturbance does have a significant negative impact on the population. This effect could operate at two levels. The stress caused by interactions with humans could reduce the survival or reproductive success of gorillas in areas of high disturbance, so that fewer gorillas were found there. Secondly, the individual gorilla groups could range in a such a way as to avoid areas of high disturbance. Groups might be forced to use sub-optimal habitat, for example at higher altitudes (Aveling & Harcourt, 1984). This could also cause stress and lower reproductive rates.

In conclusion, a negative correlation was found between signs of gorilla use and signs of illegal human users of the park, indicating a negative impact of human disturbance on the population. The management implications of these findings will be discussed in detail in Chapter 6. Clearly certain areas of the Virungas are in need of better protection, particularly Mikeno, and the southern and eastern ends of the range.

Although the results of this chapter indicate that the higher numbers of snares found do not themselves have a major influence on the gorillas' use of these areas, the numbers of snares are likely to be indicative of high levels of disturbance in general. Also, the gorillas which do use these areas will be at a higher risk of being caught in snares than those elsewhere. These same areas have been pin-pointed as in particular need of protection for at least twenty years (Harcourt & Fossey, 1981; Vedder & Weber, 1983; Aveling & Harcourt, 1984; Aveling & Aveling, 1989).

CHAPTER SIX

THE CARRYING CAPACITY OF THE VIRUNGAS FOR MOUNTAIN GORILLAS: CONCLUSIONS AND DISCUSSION

6.1 ESTIMATING THE CARRYING CAPACITY

As discussed in Chapter 1, carrying capacity is an important issue in wildlife management. The most recent census found the Virunga population of mountain gorillas to be increasing (Sholley, 1991). It was therefore considered valuable to make an estimation of the carrying capacity of the area. The aim of this chapter was to make such an estimate, and to consider its implications in the context of the future potential growth of the population.

Three techniques were used to incorporate the findings of the previous chapters on the availability, quality and utilisation of mountain gorilla habitat into estimations of carrying capacity. All of these used the pattern of availability of habitats described in Chapter 2. The first method simply used the area of those habitats which were found to be usable by gorillas (Chapter 3), along with potential densities of gorillas estimated from densities found during the most recent census and from the ranging patterns of monitored groups investigated in Chapter 3. The second method predicted the sizes of the home ranges of each of the groups found in the most recent census from the relationship between group size and range size found in Chapter 3. The number of additional gorillas which could occupy the remaining habitat was then estimated. The third method relied on building potential ranges on to the pattern of available habitats, based on the relationships between habitat type and home range areas found in Chapter 3. The relationship between food density within ranges and group size was then used to predict a group size for each potential home range.

The ranges of the six monitored groups described in Chapter 3 included all of the habitats within the Virungas with the exception of Alpine. Meadow contained virtually no gorilla food, and Bamboo contained a very low food density (Chapter 2). Although Bamboo was utilised by Group 11 during the times of year when bamboo shoots were present, the food density was only slightly higher during this season. Bamboo shoots were estimated to make up just 3 % by biomass of the overall diet of Group 11 (Chapter 4). As described in Chapter 2, Karisoke tracker's reports indicated that bamboo shoots were present for a mean of 3 months per year. However, this pattern was not consistent, the range being between 2 and 4.5 months. The remaining six habitats, Subalpine, Brush Ridge, Herbaceous, *Hagenia*, *Mimulopsis*, and Mixed Forest were thus considered usable gorilla habitat. Bamboo was incorporated into the estimations in different ways according to the three methods.

The area of Mixed Forest to the west of Mount Mikeno (18 km^2) was excluded for two reasons. Firstly, this area was not surveyed and is at a lower altitude than other areas, so there is some doubt as to the nature of the vegetation there. Secondly this area extends down to a main road, has human habitation all around it and has undoubtedly suffered much disturbance. In particular since the large influx of refugees from Rwanda into camps in the area in 1994, large scale cutting of firewood has occurred here (I. Redmond, *pers. comm.*).

6.1.1 Method 1: Procedure

Firstly, the Virunga area was divided into sections as described in Chapter 5. The total number of gorillas in groups found in each section during the 1989 census was calculated. The boundaries of these areas were digitised into the IDRISI GIS system and the area of each habitat type measured for each. The total area of the six usable

habitats (i.e. excluding Bamboo, Alpine and Meadow) was calculated for each section of the Virungas, and the density of gorillas per km^2 in each was calculated.

The total number of gorillas in each of the six monitored groups (including dependent infants, which were excluded from the analyses in Chapter 3) and the sizes of the MCP home ranges were used to calculate within-range gorilla densities. The ranges of Susa group, Group 5 and Beetsme's group overlapped (Figure 3.1). The total number of gorillas in the three groups and the total area of the three ranges were therefore used to calculate one overall figure for this area. As mentioned in Chapter 3, one group of five young males utilised much of the home range of Beetsme's group, but split up during the course of the study. Apart from this, Karisoke records indicate that only one other group occasionally entered the northern edge of this area. The guides following Ndungutsi's group reported that no other groups entered this group's home range. In these cases, the presence of other groups would not therefore significantly alter gorilla densities. The degree of overlap of Group 11 and Rafiki's home ranges with those of other groups was not known.

6.1.2 Method 1: Results

The group sizes, areas of the home ranges and within-range densities of the monitored groups are given in Table 6.1. Considering first the density of gorillas calculated from the total areas of the MCP home range, three groups, Ndungutsi's, Rafiki's and Susa, have within-range densities of between 2.8 and 3.4 individuals per km^2. Of the others, Beetsme's group was considered to be smaller than would be expected on the basis of their home range, as described in Chapter 3. The home ranges of both Rafiki's group and Group 11 contained a lower proportion of usable habitat, as defined above, than those of the other groups. When within-range gorilla density was calculated using the area of usable habitat in each range, this gave a density for Group

Table 6.1. The group size (including dependent infants), MCP home range size, area of usable habitat within each range and within range gorilla density for the six monitored groups. The home range mapping procedure is described in Chapter 3. The home ranges of the Susa group, Group 5 and Beetsme's group overlapped, and data for this area combined are given. Usable habitat is defined as excluding Alpine, Meadow and Bamboo, as discussed in the text, and the gorilla density is given both per km^2 of the total home range area and of the area of usable habitat.

Group	**Group size**	**Home range (km^2)**	**Usable habitat (km^2)**	**% usable**	**Density: gorillas/km^2 total range**	**Density: gorillas/km^2 usable habitat**
Ndungutsi's group	19	6.9	6.9	100	2.8	2.8
Rafiki's group	11	4.7	1.1	23	2.3	10.0
Group 11	13	7.6	4.9	64	1.7	2.7
Beetsme's group	18	12.4	12.0	97	1.5	1.5
Group 5	34	10.0	9.9	99	3.4	3.4
Susa group	34	11.8	9.6	81	2.9	3.5
Beetsme/ Group 5/ Susa combined	86	28.6	25.9	91	3.0	3.3

11 of 2.7 per km^2. A large percentage (73 %) of the home range of Rafiki's group consisted of Bamboo, and excluding this area gave a very high density (10.0 per km^2). This range was in the lowest part of the Bamboo, where it became mixed with Mixed Forest and was likely to provide more gorilla food than elsewhere. The area of usable habitat within the home range would thus have been larger, giving a lower gorilla density.

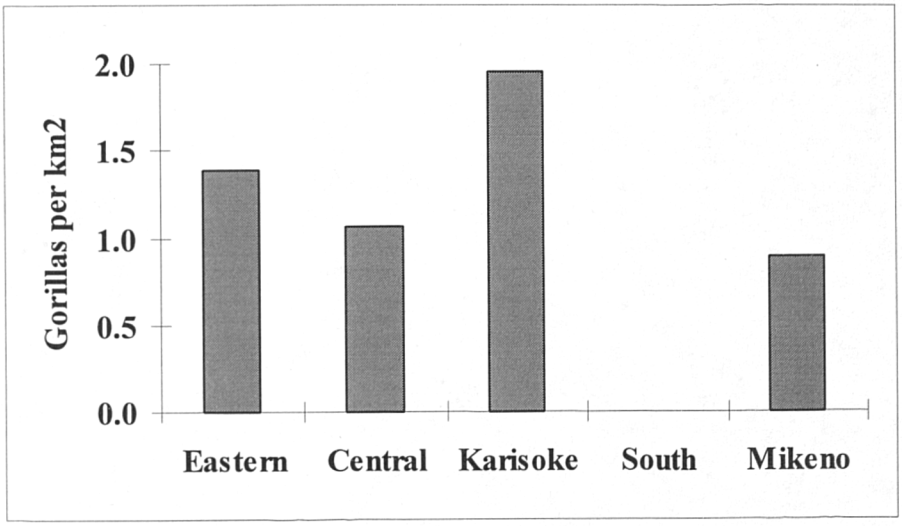
The numbers and densities of gorillas found in the five sections of the Virungas are given in Table 6.2. The densities are compared in Figure 6.1. The highest density of gorillas, 1.96 per km^2, was found in the Karisoke section. Given that the ranging patterns described above indicated that the gorilla densities within ranges were between 2.7 and 3.4 per km^2 (with the exceptions of Beetsme's and Rafiki's groups, as described) a figure of 2 gorillas per km^2 of usable habitat is a reasonable, conservative estimate of carrying capacity within usable habitat. The total area of usable habitat in the Virungas is 273 km^2, which gives an overall figure of 534 gorillas for the Virungas.

There are, however, indications that even within the Karisoke section, some habitat is under-utilised at present (see Figure 3.1), indicating that densities of gorillas higher than this could be supported. The home ranges of the monitored groups fell into two overall types, as described in Chapter 3; larger groups in larger ranges within the *Hagenia*, Herbaceous, Brush Ridge and Subalpine habitats found in the higher altitude western section of the Virungas around Mounts Karisimbi, Visoke and Mikeno, and smaller groups in smaller ranges in *Mimulopsis* and Mixed Forest in the lower altitude central section between Mounts Visoke and Sabinyo. The ranging data in Table 6.1 indicate potential densities of 3.3 per km^2 (from Beetsme's group, Group 5 and Susa group combined) and 2.7 per km^2 (from Group 11 and Ndungutsi's group) for these two categories of habitat type respectively. Using these densities and the total areas of each habitat gave a second estimated carrying capacity of 817. (Even

Table 6.2. The total area and area of usable habitat of each of the five sections of the Virungas, along with the number and density of gorillas found in each area during the 1989 census.

Section	Total area (km^2)	Usable habitat (km^2)	% usable habitat	Number of gorillas	Density: gorillas/km^2 total area	Density: gorillas/km^2 usable habitat
Eastern	89	42	47	58	0.65	1.39
Central	152	102	67	109	0.71	1.07
Karisoke	69	54	78	106	1.54	1.96
South	70	34	48	0	0	0
Mikeno	44	41	93	36	0.83	0.89
Total	424	273	64	309	0.73	1.13

Figure 6.1. The density of gorillas per km^2 of usable gorilla habitat found during the 1989 census in the five sections of the Virungas described in Chapter 5. Usable habitat was defined as excluding Alpine, Meadow and Bamboo, as discussed in the text.



without making the distinction between the two overall habitat types, an overall estimate of 3 gorillas/km^2 from the ranging data gives an almost identical carrying capacity estimate of 819.) The two estimations using this method are shown in Table 6.3.

Chapter 3 found that both main study groups used habitats selectively within their ranges, such selection would also be likely to occur at the level of groups selecting a range within the overall habitat available in the area. The habitat within groups' ranges is likely to be richer than average. The densities of gorillas within ranges would therefore overestimate the densities which could be found in the overall area. A realistic carrying capacity estimate for method one would lie between the two estimates produced here.

6.1.3 Method 2: Procedure

One problem with using the population densities in particular areas as in method 1 is that censuses provide only a snapshot of the locations of groups at one point in time, and give no information on their ranging behaviour. However, the size and composition of gorilla groups found during the 1989 census of the Virunga population is given by Sholley (1991) and could be used to predict the home range size of each. The biomass of each group recorded in the census was estimated in the same way as those of the study groups, using published estimates of 200 kg for an adult male and 100 kg for an adult female (Goodall, 1977) and estimates of 75 and 50 kg for sub-adults and juveniles respectively.

A positive correlation between home range size and group biomass was found in Chapter 3. A linear regression was calculated for this relationship, so as to allow predictions of home range size to be made from group biomass. Beetsme's group was

Table 6.3. Estimation of carrying capacity by method 1, based on potential gorilla densities for each habitat, estimated A. from gorilla densities recorded during the 1989 census and B. from ranging behaviour, as described in the text.

Habitat	**Total area (km^2)**	**A. Density estimate (gorillas /km^2)**	**A. Number of gorillas**	**B. Density estimate (gorillas /km^2)**	**B. Number of gorillas**
Alpine	27	0	0	0	0
Subalpine	25	1.96	49	3.3	83
Brush Ridge	30	1.96	58	3.3	98
Herbaceous	9	1.96	18	3.3	31
Hagenia	72	1.96	142	3.3	238
Bamboo	113	0	0	0	0
Mimulopsis	20	1.96	40	2.7	55
Mixed Forest	116	1.96	227	2.7	312
Meadow	12	0	0	0	0
Total	424		**534**		**817**

excluded for the reasons detailed in Chapter 3. This regression was then used to predict the range sizes of each group, and the total area of these ranges was calculated.

As mentioned above, the home ranges of Beetsme's group, Group 5 and Susa group overlapped (see Figure 3.1). The sizes of the areas of overlap were measured using IDRISI; 33 % of the home range of Beetsme's group and 13 % of Susa group's range overlapped with Group 5's range. A total of 55 % of Group 5's range overlapped with the other two groups. A conservative estimate is thus that each group would share a 15 % overlap with two neighbouring groups. If each area of overlap between two groups' ranges was divided equally between the two groups, the effective size of each range would thus be 15 % less than the total size. The effective total area occupied by the predicted ranges of groups recorded in the census was calculated on this basis. The gorilla density within that area was calculated, and the number of additional gorillas that could be supported by the remainder of the usable habitat was estimated on the basis of that density.

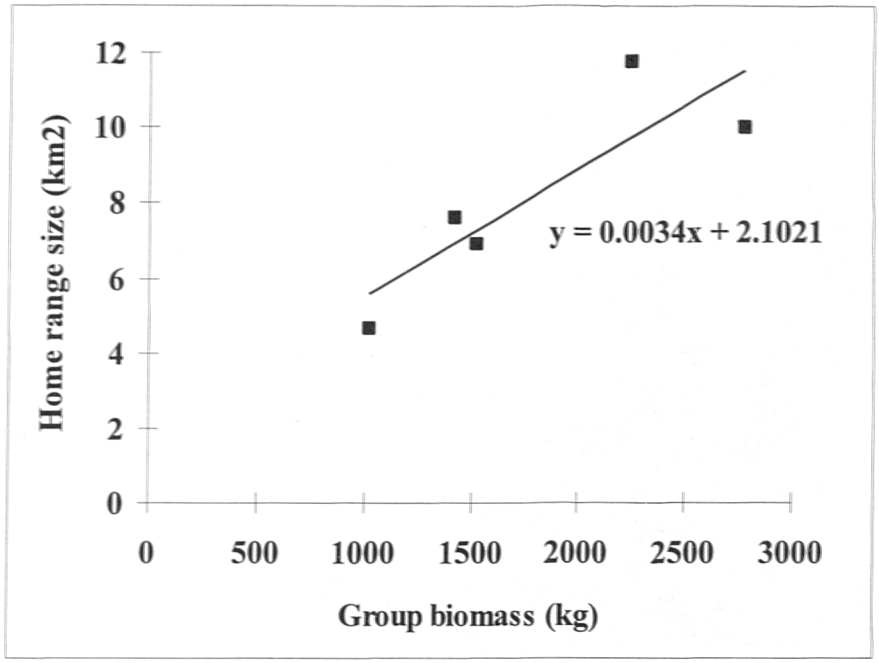
6.1.4 Method 2: Results

The relationship between group biomass and home range size in the monitored groups is shown in Figure 6.2. The regression equation was:

Home range size = (Group biomass)*0.0034 + 2.10

(with home range size in km^2 and group biomass in kg, $r = 0.86$, $p = 0.03$, $n = 5$, see Figure 3.3).

Figure 6.2. The relationship between group biomass and home range size of the monitored groups, excluding Beetsme's group. The linear regression line is shown.



The size, biomass and predicted home ranges of the 32 groups found in the census are shown in Table 6.4. The sum of the sizes of these 32 home ranges was 177 km^2. When corrected for overlap of ranges as described above, the total area was 150 km^2.

The home ranges of the monitored groups contained negligible areas of Alpine and Meadow habitats. However, in addition to the six habitat types described above as usable, they did contain Bamboo, in proportions ranging from 0 to 73 %, with a median of 10 %. If the predicted ranges of the 32 groups contained 10 % Bamboo, the total area of usable habitat (i.e. excluding Bamboo) within those ranges would be 135 km^2. The 32 recorded groups contained a total of 309 gorillas, giving a density of 2.29 per km^2 of usable habitat. With a total of 273 km^2 of usable habitat in the Virungas, this gives a carrying capacity estimate of 625 gorillas.

6.1.5 Method 3: Procedure

As mentioned above, the home ranges of the six monitored groups fell into two main types, larger ranges in the habitats in the region of Mounts Karisimbi, Visoke and Mikeno, and smaller ranges in the habitats in the lower region between Mounts Visoke and Sabinyo. The home ranges of these six were first superimposed over the habitat map of the Virungas presented in Chapter 2. Additional potential ranges were then added to the map, based on the two observed types of home range and according to the following principles:

1. Ranges were convex polygons, as the findings on ranging behaviour on which these predictions were based used a minimum convex polygon technique to estimate home range area.

Table 6.4. The group sizes of the 32 groups recorded during the 1989 census of the Virunga population and home range sizes predicted for each using method 2 (see text), based on the relationship between group size and home range size shown in Figure 6.2.

Group[1]	Group size	Biomass (kg)	Home range size (km^2)
1	7	725	4.57
2	4	400	3.46
3	8	700	4.48
4	4	575	4.06
5	6	800	4.82
6	2	400	3.46
7	11	1325	6.61
8	3	425	3.55
9	6	625	4.23
10	6	1100	5.84
11	14	1175	6.10
12	7	700	4.48
13	10	1175	6.10
14	5	525	3.89
15	10	1275	6.44
16	15	1450	7.03
17	12	1075	5.76
18	6	625	4.23
19	27	2650	11.11
20	6	1075	5.76
21	34	2800	11.62
22	13	1250	6.35
23	23	2150	9.41
24	10	975	5.42
25	11	1175	6.10
26	6	950	5.33
27	4	475	3.72
28	13	1550	7.37
29	5	600	4.14
30	2	400	3.46
31	6	650	4.31
32	7	575	4.06

[1] groups numbered as in Sholley (1991).

2. Ranges sizes were between 10 and 13 km^2 in the *Hagenia*, Herbaceous, Brush Ridge and Subalpine habitats in the area around Karisimbi, Mikeno and Visoke, and between 6 and 8 km^2 in the remainder of the Virungas. These figures were based on the ranges sizes of the monitored groups in each area (see Table 6.1). Although the home range of Rafiki's group was estimated to be smaller, 4.7 km^2, it was decided to err on the side of caution and use a minimum of 6 km^2, rather than assuming that other groups could occupy such a small home range.

3. Alpine and Meadow habitats were not included except where unavoidable in maintaining the convex polygon shape. Bamboo was included in potential ranges, as along as a minimum of 25 % of other usable habitats was also included (as in the home range of Rafiki's group, which had the highest proportion of Bamboo of the monitored groups). Extensive areas of continuous Bamboo were thus avoided. The low food density in ranges containing Bamboo was accounted for by using food density to predict group size.

4. Ranges of adjacent groups could overlap up to a maximum of 30 % (as described above, see method 2) of the area of any one group.

Group biomass was found to be correlated with food density within the home range in Chapter 3. A linear regression was calculated, using group size rather than biomass, as the aim was to estimate the carrying capacity in terms of numbers of individuals. As in Chapter 3, group sizes used did not include infants, as they were not considered to contribute significantly to group biomass or food intake. Beetsme's group was again excluded for the reasons described in Chapter 3. The polygon boundaries of each range were digitised into the IDRISI system and the area of each habitat type within each range measured, as described for the monitored groups in Chapter 3. A weighted average food density in each was estimated from the food density in each habitat, from Chapter 2, weighted by the area of each habitat. The regression

equation was then used to predict the size of the group occupying each potential range.

6.1.6 Method 3: Results

The relationship between group size and food density found is shown in Figure 6.3. The regression equation was:

Group size = (Food density)*0.29+7.20

(where group size is number of individuals and food density * 1000 kg/km^2, $r = 0.97$, $p = 0.0033$, $n = 5$)

The pattern of ranges produced using this method is shown in Figure 6.4. The gaps in the pattern are areas of non-usable habitat, mainly Meadow, Alpine, and extensive continuous areas of Bamboo. Although gorilla groups could utilise such areas of bamboo during at least some bamboo shooting seasons, they would not fall within the usual home ranges.

The home range sizes, food densities within home ranges and predicted group sizes of these groups are given in Table 6.5. The total predicted number of gorillas in these groups, excluding infants, was 458. Infants make up 17 % of the population according to the most recent census data (Sholley, 1991); allowing for this gave 551 gorillas. When this was added to the 129 in the six monitored groups, a carrying capacity estimate for the Virungas of 680 gorillas was obtained.

Figure 6.3. The relationship between food density within the home range and group size in the monitored groups, excluding Beetsme's group. The linear regression line is shown.

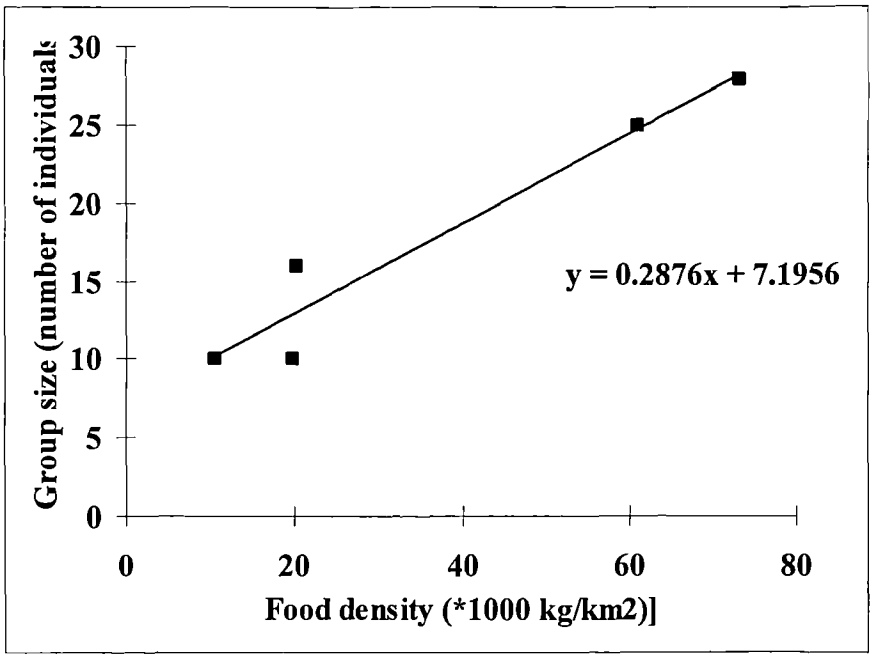


Figure 6.4. The MCP home ranges of the six monitored groups, with the pattern of potential ranges constructed using method 3 (see text). The grey outline represents the forested area of the Virungas. Predicted group sizes are indicated by the size of circle. The six monitored groups are shown in white and the predicted groups in black.

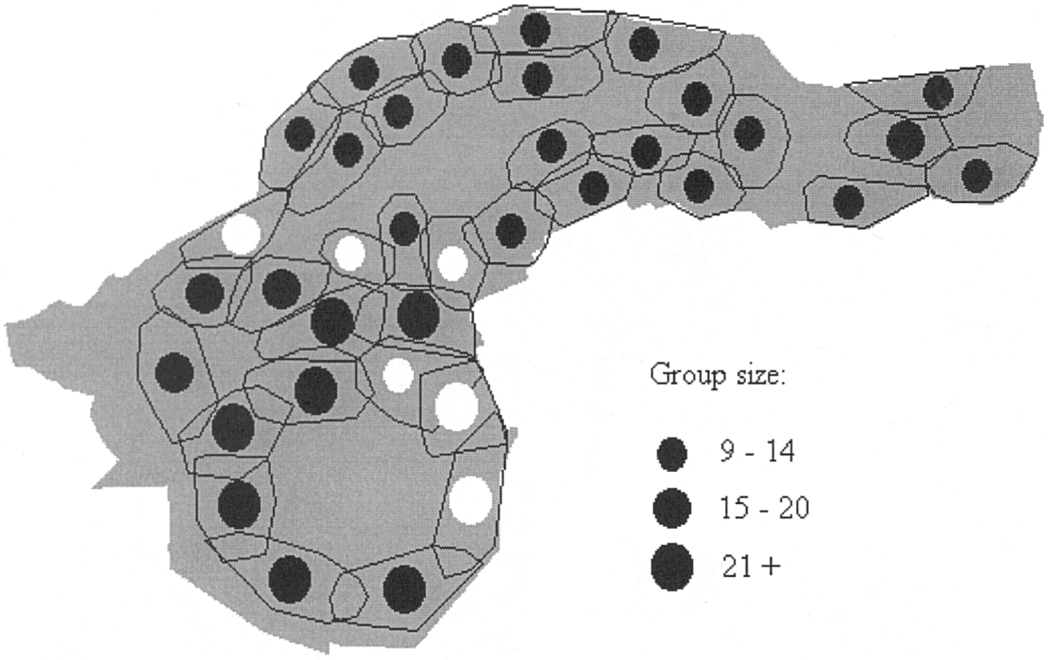


Table 6.5. The sizes and food densities of the potential home ranges constructed using method 3 (see text), with the size of each group predicted from the relationship between food density and group size shown in Figure 6.3. Data on the six monitored groups are given for comparison.

Group	Range size (km^2)	Food density (*1000 kg/km^2)	Group size (excluding infants)
A	13.0	53.7	22.8
B	12.8	51.0	22.0
C	11.1	58.7	24.2
D	11.2	58.3	24.1
E	12.2	67.3	26.7
F	10.9	47.3	20.9
G	11.2	40.1	18.8
H	10.9	66.1	26.4
I	8.4	26.1	14.8
J	8.0	6.4	9.1
K	6.4	11.2	10.4
L	8.1	28.7	15.5
M	7.5	6.9	9.2
N	6.4	9.9	10.1
O	6.3	8.9	9.8
P	6.2	16.6	12.0
Q	8.3	15.8	11.8
R	8.3	20.7	13.2
S	7.6	20.6	13.2
T	8.0	20.4	13.1
U	8.0	20.9	13.3
V	6.9	20.9	13.3
W	8.0	20.9	13.3
X	8.4	20.9	13.3
Y	8.1	20.3	13.1
Z	7.9	14.3	11.4
A'	6.9	13.7	11.2
B'	6.8	18.4	12.5
C'	7.0	29.5	15.7
D'	7.5	20.9	13.3
Susa group	11.8	61.1	25
Group 5	10.0	73.2	28
Beetsme's group	12.4	62.1	13
Group 11	7.6	19.6	10
Rafiki's group	4.7	10.4	10
Ndungutsi's group	6.9	20.1	16

6.1.7 Carrying capacity estimates: comparisons of three methods

The most straight forward method, method one, gave two different estimates depending on the potential gorilla density estimate used. As discussed, the most appropriate carrying capacity estimate for method one lies between these two. This method assumed that although gorillas utilise Bamboo to some extent, it was the six habitats defined as usable at the outset which supported the density of gorillas in the reference areas.

Method 2 utilised the relationship between group biomass and home range size based on ranges which did contain Bamboo. Two of the monitored groups' home ranges contained considerably larger proportions of Bamboo than the median figure of 10 % used in the calculations, suggesting that more of the total area of Bamboo could contribute to the predicted ranges of the groups recorded in the census. However the overall aim was to make a conservative estimate of carrying capacity, and in the light of this the best strategy was to use the 10 % figure based on the ranges of the monitored groups. One problem with this method is that the biomasses of 23 out of the 32 groups recorded in the census were outside the range of biomasses of the monitored groups used to calculate the regression equation on which home range size estimates were based. Regression equations should not generally be used to make predictions which extrapolate beyond the range of values originally used to calculate the equation (Zar, 1984).

Method 3 is the most realistic method, in that it uses not only the areas of habitats, but their configuration within the Virungas as well. The relationship between food density and group size on which the predictions were based was the strongest correlation between the variables investigated in Chapter 3. In addition, the estimated food densities in the potential ranges were generally within the range found within the home ranges of the monitored groups on which the regression was based. The only

exceptions were four home ranges with slightly lower food densities (less than 10 % outside the range observed in monitored groups). The predictions of group size were therefore considered reliable.

Table 6.6 summarises the carrying capacity estimates made using the three methods detailed above. Overall, methods 2 and 3 gave similar estimates of carrying capacity (625 and 680 gorillas), both of which were within the range of values indicated by method 1. Rounding down, it can be concluded that based on the availability of habitats within the Virungas and the observed patterns of ranging and habitat use, the area could support a conservative estimate of 600 gorillas.

6.2 DISCUSSION

6.2.1 Assumptions of the comparative approach

The approach taken to estimating carrying capacity was a modification of the comparative approach described by Bell (1984). Two assumptions underlie this approach. Firstly the vegetation classification system must allow habitats with similar carrying capacities to be correctly identified as such; in other words, like must be compared with like. In this study, the vegetation of the Virungas was classified into nine habitat types, allowing distinctions between habitats to be made at a finer level than the simple description of montane forest, which includes a heterogeneous variety of vegetation types (White, 1978). Although the classification was subjective, the habitat types were readily identifiable from aerial photographs and a large proportion of the area was surveyed (Figure 2.1). The fact that gorillas were found to distinguish between these habitat types, utilising them selectively (Plumptre, 1991; Watts, 1991; Chapter 3) indicates that the classification was relevant to their ranging behaviour.

Table 6.6. Summary of the carrying capacity estimates produced using the three methods described in the text.

Method	Estimate	Comments
1a	534	estimated from densities found during the 1989 census
1b	817	estimated from densities calculated from ranging data
2	625	estimated using the relationship between group size and home range size and the sizes of groups found during the 1989 census
3	680	estimated by building potential home ranges on the pattern of available habitat, and using the relationship between food density within ranges and group size

The second assumption is that the reference area on which predictions are based must themselves be at carrying capacity. This then begs the question as to how carrying capacity is actually defined. As discussed in Chapter 1, there has been considerable confusion surrounding this concept (Dhondt, 1988). If the aim is to establish the maximum density of animals that can be sustained in an area, without external interference or predation, and without regard to the condition of the animals in the population, then the reference area has to be at ecological carrying capacity (Bell, 1984). Other management aims would modify this prerequisite. In this study, the stated aim was to obtain a conservative estimate of carrying capacity, that is of how many gorillas the Virungas could support, assuming current patterns of habitat use are maintained and by implication without significant reductions in the condition of the population or degradation of the habitat. That the second assumption was met is therefore a tautology.

6.2.2 Is the population below carrying capacity?

The estimate of carrying capacity made indicates that the current estimated population of 324 individuals could at least roughly double in size. Several other lines of evidence support the conclusion that the population is below carrying capacity. Firstly, the population is actually increasing (Sholley, 1991), and at a faster rate than expected. Weber & Vedder (1983) modelled the potential growth rate of the Virunga population based on demographic rates observed in the Karisoke study groups and on the age/sex structure of the population from census data, and predicted that the population could grow at 1.7 % per annum. On that basis, the census count of 279 individuals in 1986 (Aveling & Aveling, 1989) should have risen to 293 individuals by 1989, when 309 were actually counted (Sholley, 1991). While it is possible that the difference was due to a more thorough count in the 1989 census, both studies

estimated that they had made a 5 % underestimate, and there is little doubt that there is an upward trend in the population (Figure 1.2).

Secondly, the pattern of available habitat described in Chapter 2, when compared with the distribution of gorilla groups found during the most recent census, indicates that there are significant areas of potential habitat unused, particularly on the southern side of Mount Karisimbi and in the central saddle region between Mounts Visoke and Sabinyo. This observation was a major impetus behind this study, and suggested the approach taken in estimating carrying capacity.

Thirdly, within the Karisoke study area, Plumptre (1991, 1995) concluded that the gorilla population was below carrying capacity, as the pattern of dietary selection relative to the availability and nutrient content of food items indicated that food was not limiting the population. Plumptre (1991, 1994) also found that trampling damage by large herbivores in the area had little effect on the biomass of food plants available.

6.2.3 Interpretation of the estimate obtained

Given that the population is below carrying capacity and is therefore expected to continue to rise if given sufficient protection, models of population dynamics and plant-herbivore interactions allow predictions to be made of the behaviour of the population, along with interpretations of the meaning and implications of the carrying capacity estimate obtained in this study.

The logistic model of population growth rate predicts a sigmoid growth curve, with the rate of population growth decreasing as the population rises to an asymptotic level, *K*, which has been considered equivalent to carrying capacity (e.g. Odum,

1953; Caughley & Sinclair, 1994). In this model, carrying capacity, *K*, is the equilibrium reached where a population is limited by resources, in the absence of external influences such as predation or hunting. Intraspecific competition for resources is assumed to regulate populations, in a density-dependent way, by increasing mortality and/or decreasing fecundity, as has been shown in, for example, African buffalo, *Syncerus caffer* (Sinclair, 1977) and olive baboons, *Papio anubis* (Strum & Western, 1987). This study used a different definition of carrying capacity, being the number of gorillas the Virungas could support, assuming current patterns of habitat use are maintained and by implication without significant reductions in the condition of the population or degradation of the habitat. The underlying assumption is that the resources available per individual would not be reduced if the relationships between group size, food density and home range size observed among the study groups were maintained. This definition of carrying capacity, and the estimate of 600 gorillas based on it, will therefore be lower than the equilibrium predicted by the logistic model, where resources would limit the population. It can best be interpreted by concluding that the Virungas can support *at least* 600 gorillas.

Caughley (1976, 1979) adopts a different approach to modelling plant-herbivore dynamics, based on the fact that plants and herbivores exist in interactive systems and should not be treated in isolation. This system can be broken down into two main components, firstly the rate of intake of plant material by a single individual as a function of the standing crop of vegetation, and secondly the rate at which the herbivore population increases as a function of the standing crop of vegetation. The former is termed the functional response and the latter the numerical response. These two components can be used to model the behaviour of the system. Any system will tend to reach an equilibrium at which the rate of production of forage is equal to the rate of off-take. In the absence of external influences this equilibrium represents the ecological carrying capacity. Other equilibria can be reached at lower population levels through regulation by, for example, predation or a harvest off-take.

There is no basis for assuming that the Virunga gorilla population would reach an equilibrium at 600 individuals. The upward trend in the population indicates that there is no such equilibrium at present, and the estimate of 600 gorillas was obtained on the assumption that current patterns of resource utilisation would be maintained, as described above. The utilisation of resources would not be expected therefore be expected to balance their production at that level. Only when the rate of resource utilisation increased to equal the rate of production would an equilibrium be expected. In the absence of external influences, the gorilla-plant system would thus be expected to reach an equilibrium at a higher level than the estimate of 600 individuals. In the case of the Virunga population, where non-human predation has been unknown since 1961 (Tobias, 1961; Schaller, 1963), this would mean in the absence of human disturbance. However, Caughley's (1976) model also suggests that an equilibrium can be reached below ecological carrying capacity, if maintained by external forces. There is evidence of a human imposed off-take in the Virunga gorilla population. In monitored groups on the Rwandan side, two individuals died as a result of snare wounds in 1988 and 1991. In 1991, nine cases were reported of gorillas being caught in snares. Seven of these required veterinary intervention, six of which were successfully treated and released (Macfie, 1992); the other died from its wounds. This suggests that in non-monitored groups (approximately half of the population), where interventions are not possible, snare-related deaths are likely to be more common. In addition, it was concluded in Chapter 5 that human disturbance influences the distribution and/or ranging patterns of the gorillas, and could thus have a negative impact on the reproductive or mortality rates through the mechanisms discussed. It is possible, therefore, that an equilibrium could be reached below the estimate of carrying capacity obtained in this study.

6.2.4 Potential for increase beyond the estimated carrying capacity

It is hard to predict at what level beyond the estimated 600 individuals the population would reach an equilibrium in the absence of human disturbance. The level would depend on which factors and mechanisms limited the population. If intraspecific competition for food were to limit the population, the equilibrium level would depend on how patterns of diet and ranging changed as the population increased, that is on to what extent the gorillas could adapt their diet to utilise a greater proportion of the available plant biomass, and could utilise smaller home ranges. Home range size has been found to be inversely related to population density in howler monkeys, *Allouatta* spp. (Crockett & Eisenberg, 1987) and in Colobus monkeys, *Colobus guereza* (Dunbar, 1987).

Several studies have found diet to become less selective or to include lower quality food items at or above carrying capacity. For example, giant pandas were found to show decreased dietary selection when the carrying capacity of the habitat was reduced after mass-flowering and die off of the preferred species of bamboo (Reid *et al.*, 1989). Feral donkeys, *Equus asinus*, in northern Australia consumed a lower quality diet in a population at carrying capacity than in a growing population below carrying capacity (Freeland & Choquenot, 1990).

In mountain gorillas, Watts (1984) found that the diets of individuals within one group showed less overlap in habitats with lower food density, suggesting an ability to diversify the diet in response to increased competition for food. It was found in Chapter 4 that Group 11, whose home range contained a lower food density than Beetsme's group, did have a slightly broader diet, although the difference was not large. A detailed examination of the nutrient content of the diet of gorilla groups occupying different quality habitats would give some indication as to what extent the

gorillas could utilise a lower quality diet in response to the increased feeding competition which would be associated with increased population size.

In addition to competition for resources, social factors could limit the population. Increased intraspecific competition can result in increased levels of aggression (Petocz, 1973). Social factors have been shown to limit pride size, and thus population density in lions, *Panthera leo* (Bertram, 1973). In mountain gorillas, intergroup encounters can result in infanticide (Watts, 1989), so that an increased density of groups would cause increased infant mortality. In addition, more frequent intergroup encounters could caused increased stress and lower reproduction or increase mortality. Although gorillas are not territorial at current population densities, other groups rarely enter the core areas of particular groups (Fossey & Harcourt, 1977) and tolerance of neighbouring groups could decrease at higher population densities.

According to the logistic model, the rate of population increase is gradually reduced by density-dependent regulation as the population increases. According to the definition of carrying capacity used, with a gorilla population of 600 individuals in the Virungas, intraspecific competition for resources would not be significantly higher than in the current population of approximately 300. This would suggest that the population would rise considerably beyond 600 before reaching an equilibrium. However, Fowler (1981) suggested that density-dependent responses in large mammals are only expressed at population levels close to the ecological carrying capacity. If this were the case, an equilibrium could be reached at a level closer to the estimate of 600 individuals obtained in this study. Social factors might operate in limiting the population at any level above 600, as above this point gorilla densities would increase beyond the observed levels used to calculate this figure.

In reality, few wildlife populations ever reach a constant equilibrium. Richard (1985) reviewed studies of primate populations, all of which showed fluctuations over time. Populations can rise above carrying capacity when released from some constraint, such as hunting, or when introduced into a new area before the availability of food is lowered enough to reduce the growth of the population. Typically a population crash follows such an eruption, and oscillations may continue with or without an equilibrium being reached (Caughley, 1970, 1979). Delayed density-dependent regulation can cause populations to fluctuate, as with Soay sheep, *Ovis aries* (Clutton-Brock *et al.*, 1991) and red grouse, *Lagopus lagopus* (Watson & Moss, 1971) where winter mortality depends on the population size during the previous summer. Herbivore populations may exhibit cycles with or without the presence of predators (Petersen *et al.*, 1984). Environments fluctuate to varying degrees, which can cause wide fluctuations in herbivore populations, particularly in arid regions with a large variation in rainfall (Caughley, 1987; Caughley & Sinclair, 1994). Rainfall is high in the Virungas (2000 mm per year) and although there is variation both seasonally and between years (Watts, 1984; Plumptre, 1991), no evidence of seasonal fluctuations in plant growth rates has been found (Plumptre, 1991). This suggests a constant environment which could allow a relatively stable population equilibrium to be reached. However, without continued monitoring of the population changes and investigation of the mechanisms of population regulation, detailed predictions of the behaviour of the population as it approaches carrying capacity are not possible.

6.3 MANAGEMENT IMPLICATIONS

The Virungas were first designated as a national park, the first in Africa, in 1925 by King Albert of Belgium with the intention of protecting the gorilla population. The management aims at present, however, include the protection of the entire ecosystem, with its associated genetic and ecological diversity, as well as limited recreational

access, scientific research and education (d'Huart *et al.*, 1985). The gorillas, being one of the main large herbivores, are an important part of the ecosystem. In addition, the income from tourists, who visit the region primarily to see the gorillas, pays for the maintenance of the national parks in both Rwanda and Zaire and is an important factor in the local and national economies (Harcourt, 1986; Aveling & Aveling, 1989). The protection and management of the gorilla population is thus an integral part of the conservation of the ecosystem.

In addition to the estimate of carrying capacity obtained, several of the findings from this project are relevant to the management of the Virungas ecosystem. An improved understanding of the availability of potential gorilla habitat was obtained, and the population was found to utilise a broader range of habitats than had previously been documented. Dietary patterns indicated a considerable degree of flexibility in the actual foods consumed, and an ability to broaden the diet to some extent. This allows different habitats to be occupied, including those with a lower density of food available than the well-studied habitats within the Karisoke study site.

The pattern of availability of habitats, along with the current distribution of gorillas allow particular sections of the forest which could support larger populations to be identified. A large area of potentially good habitat exists on the southern and western sides of Mount Karisimbi with no gorilla population. According to the potential distribution of gorillas groups constructed in this chapter (method 3, Figure 6.4) over 90 gorillas could occupy this area. In addition, the large saddle area between Mounts Visoke and Sabinyo contains a larger area of usable habitat than previously thought (Weber & Vedder, 1983), and could support an increased gorilla population. A more detailed study of the habitat quality and gorilla ecology in the lowest parts of this area on the Zairean side would be valuable in assessing further the importance of this area.

Human disturbance was found to have a negative impact on the gorilla population. This emphasises the importance of protecting the entire area, if the population is to continue to grow up to the predicted level. Indications from the most recent census of which areas contained high densities of snares allow particular sections to be identified as in need of improved protection. Significant numbers of snares were found on the south side of Karisimbi, in the area around Mikeno and in the eastern section of the Virungas. All of these regions, particularly Mikeno, have suffered heavily from human disturbance in the past (Harcourt & Fossey, 1981; Weber & Vedder, 1983; Aveling & Harcourt, 1984).

The potential population growth rate estimated by Vedder & Weber (1983) was 1.7 % per year. At that rate, the current population of 324 would rise to the conservative estimate of carrying capacity (600 individuals) obtained in this study by the year 2026. If the counts from the last two censuses (1986 and 1989) are assumed to be accurate, the current growth rate is actually considerable higher, at 3.4 %. In this case the 600 figure could be reached by 2011. Although currently below carrying capacity, the population could clearly approach that level in the foreseeable future, with associated management implications.

As discussed in Chapter 1, the management aims for a given species determine what is a desirable population level and thus the definition of carrying capacity used. For a number of reasons, a safe conservation strategy might be to maintain a population below ecological carrying capacity. The conservative definition of carrying capacity used in this study would then be appropriate. As mentioned above, populations at ecological carrying capacity will be in poor condition (Freeland & Choquenot, 1990), with resource limitation reducing the rate of population growth to zero by increasing mortality and/or decreasing reproductive rates. In such a condition, individual animals will be more susceptible to diseases, and the low reproductive rates would could make the population less able to recover from catastrophe. Wildlife

populations rarely reach a constant equilibrium at carrying capacity, but fluctuate to a varying degree around that level because of changes in environmental conditions and intrinsic demographic stochasticity (Caughley & Sinclair, 1994). Such stochasticity is particularly important in small populations such as the Virunga mountain gorillas. A population close to ecological carrying capacity will be more likely to exceed it through such fluctuations. The adverse effects on habitat of populations above carrying capacity and subsequent crashes of those populations have been documented, for example, in the elephant population in Tsavo National Park, Kenya during the 1960s and 1970s (Corfield, 1973).

There are several reasons to consider the Virunga mountain gorilla population to be particularly vulnerable. Small, isolated, populations and low reproductive rates have been widely recognised as increasing the risk of extinction (Soulé, 1987; Burgman *et al.*, 1993; Caughley, 1994). Populations of primates that live in small family groups, such as gorillas, are at greater risk of extinction through demographic stochasticity than species which live in extended groups (Dobson & Lyles, 1989). Soulé *et al.* (1979) predict that many species existing in isolated protected areas in East Africa, such as the Virungas, are likely to go extinct without active management. Continued monitoring of the population is critical, particular as it approaches carrying capacity. Detecting changes in the patterns of plant-herbivore interactions will allow action to be taken before problems arise.

This thesis has concentrated almost exclusively on the ecology of the gorilla population as related to the habitat within the protected forest area of the Virungas. However, the external threats to the population, particularly in the face of the current unrest and fighting in Rwanda, undoubtedly pose the greatest threat to the population at the present time. The area around the Virungas is the most densely populated part of Rwanda, which is the most densely populated country in the Africa. With over 400 people per km^2 (Harcourt, 1986) there is enormous pressure on the land around

the park and the situation is little better in Zaire and Uganda. Since the outbreak of war in 1990, fighting has continued sporadically in the forest, parts of which have been mined. However, if the population is to survive in the long term, both external and internal influences on the population must be understood and addressed. The fact that the population is considerably below carrying capacity, and thus in good condition and growing quickly, suggests that it should be well placed to recover from losses caused by the war, as long as losses are not too great and habitat is not destroyed.

Management policies, such as what action to take if the population exceeds carrying capacity, are a matter for sovereign governments (McNeely, 1992) and should be based on a sound understanding of the ecosystem concerned. Research on the dynamics of populations, such as the work on carrying capacity presented here and continued monitoring of the population and habitat, is a vital tool in making such decisions.

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APPENDIX 1

Equations relating dry biomass of leaf in grams to length of plant stem (cm) for herbaceous plants used in the vegetation surveys described in Chapter 2. All except *Boehmeria platyphylla* are taken from Plumptre (1991). Height was measured from the meristem at the apex of the plant to ground level and all leaves were collected, dried and weighed. The number of samples (n) and regression coefficient (r) are given for each equation. All regressions were highly significant ($p < 0.001$).

Laportea alatipes:

Leaf mass = $0.057*(\text{height})^{0.84}$

$n = 43$, $r = 0.90$

***Carduus* spp.:**

0-36 cm :

Leaf mass = $6.06*10^{-3}*(\text{leaf length})^{1.618}$

$n = 45$, $r = 0.98$

37 cm + :

Leaf mass = (0.10*leaf length)-2.00

$n = 27$, $r = 0.94$

***Rubus* spp.:**

Leaf mass = (0.21*stem length)-4.85

$n = 26$, $r = 0.94$

***Boehmeria platyphylla* :**

Leaf mass = (0.16*height)-5.63

$n = 15$, $r = 0.83$